Revision of the Small Tropical Whipsnakes Previously Referred to *Demansia olivacea* (Gray, 1842) and *Demansia torquata* (Günther, 1862) (Squamata: Elapidae)

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ABSTRACT. *Demansia olivacea* and *Demansia torquata*, as used by recent authors, are composite. Nine species are recognized based on coloration and morphology, with evidence of sympatry between several pairs of species. *Demansia olivacea* is restricted to the northern Kimberley and the Top End of the Northern Territory and *D. torquata* to eastern coastal Queensland. *Demansia calodera* Storr, 1978 and *Demansia rufescens* Storr, 1978, originally described as subspecies of *D. olivacea*, are raised to full species. *Demansia angusticeps* (Macleay, 1888), previously regarded as a synonym of *D. olivacea*, is resurrected for populations in the southern Kimberley, and *D. flagellatio* Wells & Wellington, 1985 is validated as a species restricted to northwest Queensland. Three new species are described.

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The whipsnakes (*Demansia*) of Australia and New Guinea are a distinctive group of medium to large, elongate, largeeyed, diurnal, fast-moving saurophagous snakes (Shine, 1980). They have proved to be one of the most taxonomically and nomenclaturally confusing genera of Australian elapids (Shea, 1998), even after the removal from *Demansia* of the brown snakes, referred to *Pseudonaja* by Worrell (1961a). By the end of the nineteenth century, ten names had been proposed, with four species recognized by Boulenger (1896). Subsequent work has shown that two of the species recognized by Boulenger were not only composite, but in some cases specimens of a single species were identified as two or more taxa (Shea, 1998). Loveridge (1934, 1949)

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and Kinghorn (1942) were unable to resolve species boundaries in *Demansia* and suggested that only a single species (*psammophis*) be recognized, although Loveridge (1949) suggested that a northern subspecies (*olivacea*) might be recognizable on the basis of greater numbers of subcaudal scales when larger samples became available. More recent work with larger series of specimens, together with field observations of sympatry between taxa, has partly resolved the taxonomy of the genus (Worrell, 1952, 1956, 1961a,b, 1963; Storr, 1978; Shea, 1998), with ten species or subspecies recognized by most modern authors (Storr *et al.*, 1986; Wilson & Knowles, 1988; Mirtschin & Davis, 1992; Ehmann, 1992; Cogger, 1996; Wilson & Swan, 2003).

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Despite this recent work, there remains much confusion over the identification and consequently the distribution of two northern species, Demansia olivacea (Gray, 1842) and Demansia torquata (Günther, 1862) (Storr, 1978; Longmore, 1986; Wilson & Knowles, 1988; Mirtschin & Davis, 1992; Ehmann, 1992; Swan, 1995; Cogger, 1996; Wilson, 2005). Much of this confusion is due to the nature of the characters purported to define the species: presence (D. torquata) or absence (D. olivacea) of a dark nuchal bar, and usually an ornate gular region. The description of a southwestern subspecies of D. olivacea possessing a dark nuchal bar, D. o. calodera Storr, 1978, suggested that this character was not mutually exclusive. Further, the presence and intensity of the dark collar and other coloration features varies with age, with larger specimens losing the strikingly contrasting colours of juveniles. Finally, it has become evident with the much larger samples of small tropical whipsnakes now available that both species, even with the exclusion of the two western taxa differentiated from D. olivacea by Storr (1978), are composite.

Our studies on the systematics of these whipsnakes began in 1980, when the junior author studied the collared whipsnakes of northeastern Australia, examining specimens in the Australian Museum and Queensland Museum. He recognized three allopatrically-distributed species in this region, one of which was named *Demansia flagellatio* by Wells & Wellington (1985). In 1995, the senior author examined all other Australian collections, and found that one of the species recognized by Scanlon extended west as far as the east Kimberley, while the northwestern populations attributed to *D. olivacea* by Storr (1978) were a composite of several readily identifiable entities.

Materials and methods

All locatable specimens of small northern Australian whipsnakes in the following collections were examined: Australian Museum, Sydney (AM); American Museum of Natural History, New York (AMNH); Australian National Wildlife Collection, CSIRO, Canberra (ANWC); Natural History Museum, London (BMNH); Museum of Victoria, Melbourne (MV); Museum and Art Gallery of the Northern Territory, Darwin (NTM); Queensland Museum, Brisbane (QM); South Australian Museum, Adelaide (SAM), United States National Museum, Perth (WAM). The material examined included specimens identified in those collections as *D. calodera, D. olivacea, D. rufescens* and *D. torquata*, together with a number of specimens which were previously unidentified.

Where possible, the following data were taken for each specimen: coloration; number of ventral scales (counted according to Dowling, 1951) and subcaudal scales (not counting the terminal scale); snout-vent length (SVL, in mm) and tail length (TL, presented as a percentage of SVL for all except holotypes, where the measurement is provided), and sex, determined by dissection of gonads or existence of hemipenes. Cursory examination of smaller samples did not reveal any obvious differences in the configuration of head shields (see also Storr, 1978; Shea, 1998 for a general description of the head scutellation in the genus) or number of midbody scales (consistently 15 for the entire genus; Storr, 1978).

In describing the position of coloration markings,

scale "rows" refer to longitudinal rows of scales, the rows numbered from ventrally (first row is that bordering the broad ventral scales) to dorsally, while scale "series" refer to transverse series of dorsal body scales, numbered from the line of scales immediately posterior to the parietals. Head shields are numbered from anteriorly to posteriorly. A stripe is a longitudinally oriented marking (along the head or body), a band is a transversely oriented marking (across the head or body), and a bar is a short, broad marking transversely or obliquely oriented to the long axis of body and head that does not completely cross from one side to the other. Except where specifically noted, coloration hues are based on preserved specimens.

Sexual dimorphism in number of ventral and subcaudal scales was statistically analysed by t-tests. Sexual dimorphism in SVL and relative tail length was determined by Mann-Whitney U tests, due to the likelihood of non-normal distributions. Statistical analyses of geographic variation in morphometric and meristic characters are based on linear regressions of characters against either latitude or longitude, depending on which coordinate had the greater range of values; statistically significant relationships were visually examined from scatterplots of variables to assess the nature of the relationship. Where no sexual dimorphism was present, analyses of geographic variation were based on all available specimens; where sexual dimorphism was present, sexes were separately analysed. For these analyses, latitude and longitude were entered as decimal fractions of degrees, and relative tail length was entered as a decimal fraction (tail length/SVL). Statistical analyses were performed with the SYSTAT package (Version 7.0). In presenting the results of statistical analyses, subscripts give the degrees of freedom of a test, t is the t-test statistic and U is the Mann-Whitney test statistic. Superscripts *, ** and *** respectively refer to p < 0.05, p < 0.01 and p < 0.001. Where no probability is given for a statistical test, p is > 0.05.

Authorship of new species' names are stated for each species.

In presenting locality data, names in quotation marks are property names. It is not always clear from museum registers whether these names refer to the overall property, or just to the dwelling (homestead), although when a distance from such a name is provided, we assume that the referent is the homestead.

Results

Coloration, particularly the existence and position of markings on the head and gular region, identified several geographically cohesive groups. These groups were further differentiable in some cases on mean number of ventral and subcaudal scales and size. In most cases, each group based on coloration was allopatric to others. However, sympatry of two or more groups was observed at a few localities (detailed below). At each of these locations, the coloration and scalation features differentiating the groups were maintained, suggesting that reproductive isolation was maintained. Several other groups showed a close geographic proximity, again with no evidence of intermediacy in the characters differentiating them. Because of this lack of any intermediacy in close geographic proximity, together with the consistency of coloration over large distances, the coloration groups are treated as distinct species.

Systematics

Demansia angusticeps (Macleay, 1888)

Figs. 1-2

Diemenia angusticeps Macleay, 1888: 417. Holotype: AM R31921 (formerly Macleay Museum R712) from the vicinity of King's Sound, WA.

Diagnosis. A moderately large (SVL to 676 mm) *Demansia* lacking dark or pale nuchal collars or dark spots on anterior ventrals, but possessing a dark transrostral streak that is usually excluded from the orbit and well-developed pale pre- and postocular bars.

Description. Head dorsum grey-brown to brown, concolorous with body (nape sometimes a little darker, but not forming a discrete, sharply-demarcated dark band), snout and temporal region flushed with orange-brown; usually one large central, and sometimes additional smaller, dark macules in each internasal and prefrontal scale; well-defined narrow dark brown transrostral streak, edged white above and below, usually not reaching the orbit, but broadly angled ventrally along suture between second and third supralabial, and sometimes with extensions between first two supralabials; a dark brown teardrop marking posteroventral from eye, beginning broadly across ventral half of lower postocular and posterodorsal corner of fourth supralabial, across centre of fifth supralabial, ventral angle of temporolabial, and ending by diffusion across anteroventral corner of sixth supralabial, last two infralabials (sixth/seventh), rarely extending posteriorly along dorsal scale rows two and three;

a prominent cream preocular bar, usually separating dark transrostral streak from orbit, extending posteroventrally to edge dark teardrop anteriorly; prominent narrow cream postocular bar over anteroventral half of upper postocular, dorsal half of lower postocular, (occasionally anteroventral corner of primary temporal), dorsal quarter of fifth supralabial, ventral half of temporolabial, and diffusing over anteroventral third of sixth supralabial.

Body dorsum olive grey-brown to mid-brown, more yellow-brown on tail; more lateral dorsal scales often with dark grey spots at base; neck often with dark central spots or anterior streaks on scale rows one and two; body dorsal colour extends onto lateral edge of ventrals.

Venter yellow-cream; grey clouding along sutures between genials and infralabials, and occasionally similar grey spots and flecks in adjoining areas.

Ventrals 183–200, mean = 189.9, s.d. = 4.92, n = 31; subcaudals 74–98, mean = 84.1, s.d. = 6.93, n = 27. SVL 178–676 mm, mean = 484.4 mm, s.d. = 132.2, n = 29; TL 27.5–35.5% of SVL (mean = 31.4%, s.d. = 2.32, n = 25).

Sexual dimorphism. Males have significantly greater numbers of subcaudal scales than females (80–98, mean = 91.1, s.d. = 5.28, n = 9 vs 74–91, mean = 81.1, s.d. = 4.78, n = 14 respectively; $t_{21} = 4.723^{**}$). There are no statistically significant differences between males and females in number of ventrals (males: 184–200, mean = 191.1, s.d. = 5.24, n = 11; females: 183–197, mean = 189.1, s.d. = 5.28, n = 14; t_{25} = 0.973), TL (males: 27.5–35.2% of SVL, mean = 32.6%, n = 8; females: 28.4–35.5%, mean = 30.7%, n = 14; U = 79), or SVL (males: 180–676 mm, mean = 499.2 mm, s.d. = 174.7, n = 10; females: 178–569 mm, mean = 459.3 mm, s.d. = 108.4, n = 16; U = 112.5).



Fig. 1. Holotype of Demansia angusticeps (AM R31921).

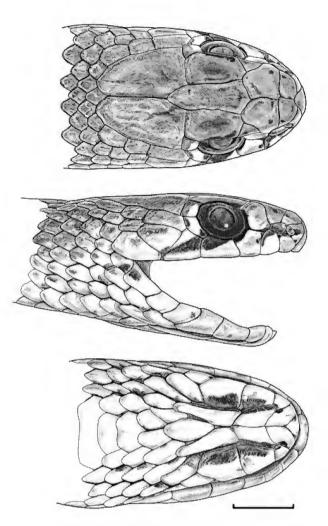


Fig. 2. Head shields and colour pattern of the head and neck of the holotype of *Demansia angusticeps*, in dorsal, right lateral and ventral views. Scale bar = 3 mm.

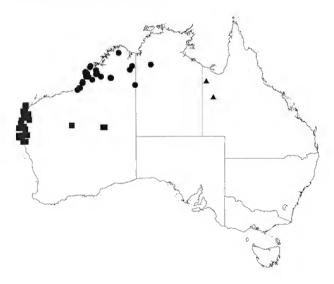


Fig. 3. Distribution of *Demansia angusticeps* (solid dots), *D. calodera* (solid squares) and *D. flagellatio* (solid triangles).

Nomenclatural history and description of holotype. *Diemenia angusticeps* was described from a single specimen collected by the entomologist and naturalist Walter Wilson Froggat from the vicinity of King's Sound (Macleay, 1888). It was synonymised with *D. olivacea* by Boulenger (1896) and remained in that synonymy (Cogger & Lindner, 1974; Storr, 1978; Cogger, 1979; Cogger *et al.*, 1983) during the transfer of application of the name *D. olivacea* from the species now known as *D. vestigiata* to the species to which is is correctly applied (Shea, 1998).

The holotype (AM R31921; Figs. 1–2) is an adult female with 196 ventrals, 81 subcaudals, SVL 519 mm and TL 152 mm.

Etymology. Although not explicitly stated by Macleay, the name *angusticeps* is presumably derived from the Latin *angustus* (narrow) and *-ceps* (head), calling attention to the long narrow head of this and other *Demansia*.

Distribution. The southern Kimberley, from 325 km SW Broome in the south, north-west to Pender Bay, north to "Old Theda" HS (the only record in the northern or central Kimberley) and east to the Victoria River valley (Fig. 3).

Geographic variation. There is no relationship between longitude and either number of ventral scales ($r^2 = 0.023$, n = 31; $F_{1,29} = 0.687$), SVL ($r^2 = 0.001$, n = 29; $F_{1,27} = 0.039$) or relative tail length ($r^2 = 0.031$, n = 25; $F_{1,12} = 0.746$), nor is there any relationship of longitude with number of subcaudal scales in either males ($r^2 = 0.008$, n = 9; $F_{1,7} = 0.054$) or females ($r^2 = 0.033$, n = 14; $F_{1,12} = 0.415$).

Specimens examined. All localities are in Western Australia: AM R31921, King Sound; R101410, old rubbish tip, N side Broome; R101433, 15.1 km NE "Broome 340 km" marker via Great Northern Hwy; R117295, 3.7 km N southern rd to "Yeeda" on Great Northern Hwy; BMNH 1931.12.2.4, Pender Bay; NTM R2077, "Victoria River Downs" HS, NT; SAM R6644, Margaret and Fitzroy Rivers, WA; WAM R10565, Liveringa; R13829, R20297, Derby; R13842, Mowanjum Mission, Derby; R20357, 23 mi. S Derby; R23018, Langey Crossing; R28067, R28069, "Frazier Downs", 10 mi. S "La Grange"; R28068, "La Grange"; R47729, "Anna Plains"; R51236, Granny Soak, E Gardner Range; R55867, "Old Theda" HS; R58539, Martins Well; R58540, 56 km NNE Broome; R60846, 1 km N Jameson Point; R60847, 4 km SE Coulomb Pt; R61355, McHugh Bore, "Dampier Downs"; R69932, Broome; R70542, 6 km 200° Turkey Creek; R75112, 12 km SE "Roebuck Plains" HS; R75113, 8 km NW Fitzroy Crossing; R79005, 27 km SSW "Anna Plains"; R85113, Wonjil Ridge; R86455, 12 km W "Mt Evelyn"; R88532, Coulomb Point.



Fig. 4. Holotype of Demansia calodera (WAM R54992).

Demansia calodera Storr, 1978

Figs. 4-5

Demansia olivacea calodera Storr, 1978: 294. Holotype: WAM R54992, from 1 km S "Tamala", WA.

Diagnosis. A small *Demansia* (SVL up to 517 mm) with a dark, pale-edged collar, the pale edges undulating and themselves edged in black, moderately narrow pale postocular bar separating dark teardrop from head dorsum, and a pale venter lacking dark markings on anterior ventrals.

Description. Head dorsum and nape light to mid brown to grey-brown, usually with a few obscure darker macules; narrow dark-brown transrostral streak, narrowly creamedged above and below, with dark extensions along sutures between first three supralabials and narrowly reaching orbit along preocular/third supralabial suture; dark to pale grey-brown to grey teardrop marking posteroventral to eye, beginning broadly at orbit across ventral half of lower preocular and posterodorsal half of fourth supralabial, arcing across central third of fifth supralabial, ventral corner of temporolabial and anteroventral third of sixth supralabial, before dissipating and fading into lateral ground colour on last two infralabials and scale rows two and three, sometimes more abbreviated, to disappear on the temporolabial; a cream preocular bar, continuous with pale edges to transrostral streak, and narrowly broken by orbital extension of that streak, extending posteroventrally to edge the dark teardrop anteriorly; prominent cream postocular bar over ventral half of upper postocular (sometimes more dorsally), dorsal half of upper postocular, ventral corner of primary temporal, dorsal corner of fifth supralabial, across middle third of temporolabial and sixth supralabial, posteriorly edging the

dark teardrop. This pale marking continuous with pale ventral coloration and with a narrow (½–1 scale wide) undulating but even-width cream band across nape on first and/or second scale series, which separates the dark head dorsum from a similarly coloured or darker grey, broad (about five scales wide) nape band, narrower laterally; junction between pale narrow nape band and broad dark nape band marked by black macules along scale margins. Dark nape band bordered posteriorly by a second, much less distinct, narrow pale nape band about half a scale wide, extending more broadly lateroventrally, where it strengthens and blends with ventral ground colour.

Body dorsum light yellow-brown; often a few fine black spots at base or apex of scales of first and second rows on side of neck.

Venter cream to pale yellow, blending gradually with browner flanks on first scale row and laterally on ventrals. Usually obscure faint grey edging to suture between genials and infralabials.

In life, an individual from "Woodleigh" HS rubbish tip, collected 5.vii.1997, had a pale yellow venter with dark edging to the hind margin of the ventrals (M. Peterson, pers. comm.).

Ventrals 171–189, mean = 180.4, s.d. = 4.60, n = 48; subcaudals 65–89, mean = 76.2, s.d. = 5.55, n = 44. SVL 137–517 mm, mean = 332.6 mm, s.d. = 94.3 mm, n = 49; TL 26.3–36.1% of SVL (mean = 30.3%, s.d. = 2.2, n = 45).

Sexual dimorphism: Males have significantly greater numbers of subcaudal scales than females (65–89, mean = 78.6, s.d. = 5.00, n = 24 vs 65–77, mean = 71.1, s.d. = 3.92, n = 12 respectively; t_{34} = 4.533***) and a correspondingly longer tail (TL 27.5–36.1% of SVL, mean = 31.3%, s.d. = 2.2, n = 24 vs 27.7–32.7%, mean = 29.5%, s.d. = 1.5, n = 12; U = 217.0*). There are no statistically significant

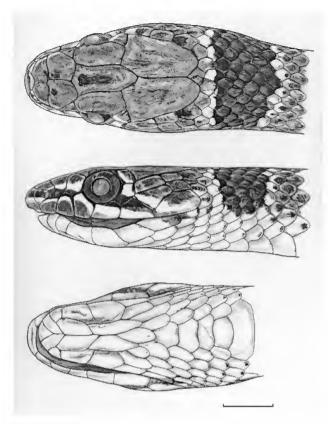


Fig. 5. Head shields and colour pattern of the head and neck of the holotype of *Demansia calodera*, in dorsal, left lateral and ventral views. Scale bar = 3 mm.

differences between males and females in number of ventrals (males: 172-188, mean = 181.2, s.d. = 3.71, n = 26; females: 172-189, mean = 179.7, s.d. = 5.69, n = 14; t₃₈ = 0.994) or SVL (males: 219-517 mm, mean = 356.3, s.d. = 86.3, n = 26; females: 257-440, mean = 358.2 mm, s.d. = 61.6, n = 14; U = 177.5).

Nomenclatural history and description of holotype. *Demansia olivacea calodera* was described from a series of 29 specimens from the Shark Bay region by Storr (1978). It was subsequently listed as a full species by Storr & Harold (1984) without further comment. The female holotype (Fig. 4–5) has ventrals 178, subcaudals 76, SVL 316 mm and TL 100 mm.

Etymology. The name is derived from the Greek καλοζ (*calos* = beautiful) and δειρη (*deire* = neck), alluding to the strong neck pattern (Storr *et al.*, 1986).

Distribution. Shark Bay and Exmouth regions of Western Australia, from "Tamala" Station in the south to Vlaming Head lighthouse in the north, and including Dirk Hartog and Bernier Islands, with an apparently isolated population in the Gibson Desert Nature Reserve (Fig. 3).

Geographic variation. The three Gibson and Little Sandy Desert specimens (WAM R108902, R112178, R135954), although over 1100 km east of the main body of the species'

range, are not noticeably different in coloration or scalation from west coastal specimens, apart from having slightly fewer subcaudal scales. The three male specimens have 175–178 ventrals, 65–72 subcaudals, SVL 276–347 mm and TL/SVL 27.5–31.7%, while males from the rest of the distribution have 172–188 (mean = 181.6) ventrals, 73–89 (mean = 79.5) subcaudals, SVL 219–517 mm (mean = 361.8 mm) and TL/SVL 28.2–36.1% (mean = 31.5%).

Storr (1978) suggested that northern populations of D. calodera had higher ventral + subcaudal scale counts (estimating total number of body segments) than southern populations, although he did not sex his material. Given that there is marked sexual dimorphism in number of subcaudal scales (but not in ventral scales), his conclusions are here reexamined. The correlation between latitude and, respectively, subcaudal scales ($r^2 = 0.181$, n = 12; $F_{1,10} = 2.212$), ventral scales ($r^2 = 0.011$, n = 14; $F_{1,12} = 0.138$) and the sum of ventrals and subcaudals ($r^2 = 0.011$, n = 12; $F_{1,10} = 0.114$) in females is non-significant in each case, although there are very few females from the north of the distribution (only one female north of 24°20'S). In males, there is a strong relationship between latitude and the sum of ventrals and subcaudals, with higher values in the north ($r^2 = 0.460$, n subcaudals, with ingret values in the norm ($1^2 = 0.406$, if = 22; $F_{1,20} = 17.012^{***}$; sum = 331.5 - 2.84*latitude). This relationship is largely due to an increase in subcaudal scales in the north ($r^2 = 0.322$, n = 22; $F_{1,20} = 9.502^{**}$; subcaudals = 122.2 - 1.72*latitude), although there is also a non-significant trend towards the same pattern in ventral scales ($r^2 = 0.121$, n = 24; $F_{1,22} = 3.040$, P = 0.095). The increase in number of subcaudal scales (and in ventral+subcaudal total) in males appears to be evenly clinal.

There are no significant relationships between latitude and either SVL (sexes pooled: $r^2 = 0.015$, n = 46; $F_{1,44} = 0.660$) or relative tail length (males: $r^2 = 0.027$, n = 22; $F_{1,20} = 0.564$; females: $r^2 = 0.097$, n = 12; $F_{1,10} = 1.080$).

Comparison with other species. *Demansia calodera* has a strong dark nuchal collar with pale edges, and is hence readily distinguishable from *D. angusticeps*, which lacks any collar. It is also much smaller than the latter species and has fewer ventral and subcaudal scales. The two species are allopatric, with the intervening area occupied by *D. rufescens*. For comparisons with other species, see subsequent accounts.

Specimens examined. All localities are in Western Australia: AM R37190, "Warroora" Stn, c. 30 mi. S Exmouth Gulf; R140521, vicinity of Denham; ANWC R1964, 70 mi. S Learmonth; WAM R4751, "Marilla"; R6530-31, "Tamala"; R11241, R13283, Bernier I.; R14055, "Wandagee" Stn; R16966, "Cardabia"; R17320-21, Quobba Pt; R22432, Eagle Pt, S of Denham; R22433, Denham; R22510-11, Vlaming Head Lighthouse; R22830, Carnarvon district; R32027-28, 2 mi. E Norwegian Bay, Ningaloo; R42378, R44237, R44546, R56099, R57096-97, Dirk Hartog I.: R44238, Herald Bay, Dirk Hartog I.; R45650, "Callagiddy", nr Carnarvon; R51027, Yardie Ck; R54587, 25 km S Denham; R54817-18, "Peron" HS; R54831, Monkey Mia; R54991, R54992 (holotype), 1 km S "Tamala"; R55098, "Eagle Bluff Well" outcamp, 20 km SSW Denham; R60476, R66300-02, "Quobba" Stn; R60526, Carnarvon; R64349, 1 km S "Tamala" HS; R71232, 37 km NE Carnarvon; R71497, 12 km NE Carnarvon; R74954, homestead turnoff, 2.5 km N "Tamala"; R76890, 0.5 km S "Gnaraloo" HS; R81770, "Wooramel" woolshed; R82771, 35 km E "Tamala" HS; R104455, Cape Range; R108902, 37.5 km to Lake Hancock, Gibson Desert Nature Reserve; R112178, Eagle Bore, Gibson Desert Nature Reserve; R113682, Notch Point, Dirk Hartog I.; R116598, 1 km W Cape Cuvier; R135954, 24°31'45"S 120°17'44"E, in Little Sandy Desert.

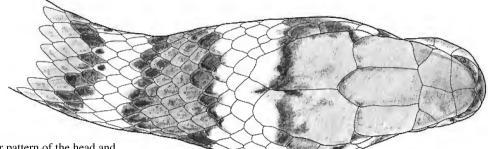
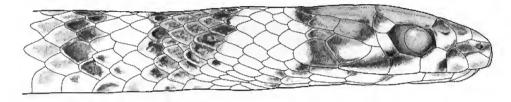


Fig. 6. Head shields and colour pattern of the head and neck of the holotype of *Demansia flagellatio*, in dorsal, right lateral and ventral views. Scale bar = 3 mm.



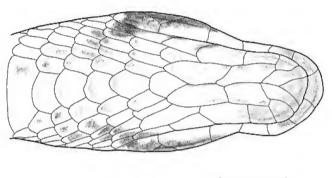
Demansia flagellatio Wells & Wellington, 1985

Figs. 6–7

Demansia flagellatio Wells & Wellington, 1985: 45. Holotype: AM R64867, Mt Isa district, Qld, collected by D. Stammer.

Diagnosis. A small, very slender *Demansia* (SVL up to 510 mm) with very long tail (subcaudals up to 115) and a bold black and yellow head pattern, including yellow postocular bar separated from broad anterior yellow nuchal band, and a second prominent black nuchal band posterior to a prominent posterior yellow nuchal band, but lacking obvious dark markings on anterior ventrals.

Description. Head dorsum and nape mid olive-brown, immaculate; prominent black transrostral streak, edged yellow above and below, posterolaterally turning ventrally along the suture between supralabials two and three, leaving at most only a narrow extension to reach orbit along suture between preocular and third supralabial; black teardrop marking ventrocaudal to eye, beginning broadly at orbit across dorsal half of fourth supralabial and ventral third of lower postocular, across middle of fifth supralabial, ventral corner of temporolabial, lower third of sixth supralabial, and last two infralabials, ending one scale posterior to the infralabial series; a prominent yellow preocular bar, usually interrupted by the orbital extension of dark transrostral streak, and continuous with the yellow edging to that streak, extending posteroventrally to edge the dark teardrop anteriorly; prominent yellow postocular bar of even width over lower half of upper postocular, upper half of lower postocular, anterior quarter of primary temporal, dorsal angle of supralabial five, and ending bluntly over middle of temporolabial or anteriorly on sixth supralabial; a weak to strong black margin to brown head dorsum, across parietals just anterior to their posterior angle, and



extending lateroventrally over part of tertiary temporal series, posterior third of temporolabial, posterior two-thirds of primary temporal, lateral angle of parietal and dorsal half of upper postocular. This dark band sharply bordered posteriorly by a broad, even-width, wide bright yellow nuchal band with weak brown clouding, over caudal angle of parietals and first two to three series of dorsal scales, continuous lateroventrally with ventral ground colour. This anterior nuchal band abruptly bordered posteriorly by a broad (4-5 scale wide) olive-brown nuchal band with moderately to strongly expressed black margins, and with posterolateroventral angle extending to most ventral row of dorsal scales. Posterior to this, a second two-scale wide yellow nuchal band, continuous with ventral colour, in turn succeeded by a narrow 1-2 scale wide black nuchal band of similar lateroventral extent to more anterior dark nuchal band.

Body dorsum olive-brown to yellow-brown.

Throat yellow, becoming more yellow-brown to pale greybrown along body, before returning to dull yellow under tail. Throat with a few black flecks and streaks, especially along lateral margins of genials, and occasionally a few obscure dark spots forming a short paired row on anterior ventrals,



Fig. 7. Demansia flagellatio from Riversleigh World Heritage fossil site, Boodjamulla (Lawn Hill) National Park; freshly-dead specimen.

extending posteriorly as far as second dark nape bar.

Colour photographs of a live individual from near Ryan Rd on the road to Lake Moondarra, just N of Mt Isa (C. Crafter, pers. comm.) show a red-brown dorsum, becoming more grey on the posterior body, then more yellow on the tail. The head dorsum and dark nape band were dull bottlegreen, edged with black, and the pale facial markings and nape bands were bright yellow. A live individual from Riversleigh had the dorsal scales tipped narrowly with red, but mainly blue-grey anteriorly and laterally, more greenish in a mid-dorsal zone and on the posterior body, and yellowbrown on the tail; the head dorsum and dark nape band were grey-brown, edged black; the eyes red (Fig. 7).

Ventrals 201–209 (mean = 204.5, s.d. = 2.88, n = 6); subcaudals 102–115 (mean = 108.0, s.d. = 4.95, n = 5). SVL 367–510 mm (mean = 424.0 mm, s.d. = 52.05 mm, n = 6); TL 38.4–41.9% of SVL (mean = 40.4%, s.d. = 1.28, n = 5).

Sexual dimorphism. Only four of the seven specimens examined were able to be sexed. All were males.

Nomenclatural history and description of holotype. Prior to its description, *D. flagellatio* was illustrated by Stammer (1976, fig. 195, although text refers to this figure as 194) and Cogger (1975), who both referred the species, either implicitly or explicitly, to *D. torquata*. As described by Wells & Wellington (1985), *D. flagellatio* was differentiated from only *D. torquata*, from which it was said to be distinguished by its more "whip-like body form", distinctive black collars, and larger size, although no specific details were given in support of these claims. Probably because of the poor description, the species has not been subsequently recognized by any author (Shea & Sadlier, 1999), although as the description explicitly compares the species with another, the name is nomenclaturally available. At least one of the purported distinguishing characters, larger size, is incorrect.

The male holotype (Fig. 6) has 202 ventrals, 115 subcaudals, SVL 377 mm and TL 158 mm.

Etymology. No etymology for the name was provided by Wells & Wellington (1985). "Flagellatio" is presumably an abstract noun formed from the Latin verb *flagellare* (to whip), with the sense of "a whipping".

Distribution. Northwestern Queensland (Fig. 3), from Mt Isa to the Riversleigh World Heritage section of Boodjamulla (Lawn Hill) National Park (a freshly-dead specimen examined by the junior author from the latter locality (Fig. 7) was unfortunately lost before lodgement in the Queensland Museum).

Comparison with other species. *Demansia flagellatio* differs from all other *Demansia* species in having a prominent black posterior nuchal band behind the second pale nuchal band. It is also generally more slender and with bolder head markings than other whipsnakes, and has the highest ventral counts of the smaller whipsnakes (exceeded only by the much larger *D. papuensis*; Shea, 1998). It is allopatric to *D. angusticeps*, and is readily distinguished from that species by possessing a bold head and nape pattern, as well as its generally smaller size. From *D. calodera*, it is distinguished by the greater breadth of the pale nuchal bands, together with the dark head dorsum, and the non-overlapping ventral and subcaudal counts. For comparisons with other species, see subsequent species accounts.

Specimens examined. AM R25982, R28455, R64867, R110400, AMNH R87692, Mt Isa, Qld; AM R153036–AM R153037, no data.

Demansia olivacea (Gray, 1842)

Figs. 8-9

Lycodon olivaceus Gray, 1842: 54. Type material: lost (formerly in British Museum, probably as part of series of specimens 41.10.13.4–45), from Port Essington, NT.

Elapocephalus ornaticeps Macleay, 1878: 221. Holotype: AM R31918 (formerly Macleay Museum R1305), from Port Darwin, NT.

Diagnosis. A small to medium-sized *Demansia* (only two records greater than 557 mm) with very reduced or absent dark transrostral streak, lips and snout greyish, finely variegated, no pale preocular bar or dark or pale collars on nape, but a median series of dark spots present on anterior ventrals (Fig. 8).

Description. Head dorsum mid-brown, concolorous with neck and body or more orange, especially over temporal region; snout finely variegated grey, brown and cream, giving an overall grey appearance; top of snout a little more coarsely variegated, and spotted brown; brown transrostral streak usually absent, or if present, weak, often broken and not edged with white; an often faint, narrow mid to dark brown teardrop marking posteroventral to eye, very narrowly edged above and below with cream, beginning over ventral half of lower postocular and posterodorsal corner of fourth supralabial, across dorsal third of fifth supralabial, ventral or middle third of temporolabial, and narrowly across sixth supralabial before diffusing and fragmenting over corner of mouth and last two infralabials; pale preocular bar usually absent, or if present, very weak and narrow; pale postocular bar usually absent, or if present generally weak and narrow.

Body dorsum brown, more yellow-brown distally on tail, sometimes with a dark basal spot on scales.

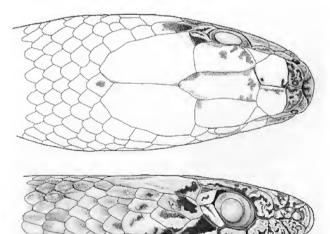
Venter dull yellow to pale bluish-yellow, the latter especially posteriorly, more bright yellow below tail; throat with coarse brown variegations, particularly along sutures, including a pair of prominent streaks along suture between genial and infralabials, and a median series of dark brown spots and bars on anterior ventrals, and in many individuals, brown spots on lateral edges of ventrals and centrally on first row of dorsal scales anteriorly.

Ventrals 168–196 (mean = 177.4, s.d. = 5.70, n = 101); subcaudals 68–106 (mean = 84.2, s.d. = 8.22, n = 91). SVL 163–643 mm (mean = 359.6 mm, s.d. = 118.7 mm, n = 101); TL 24.4–40.9% of SVL (mean = 33.2%, s.d. = 3.5, n = 89).

Sexual dimorphism. Males have slightly more ventrals (168–196, mean = 179.0, s.d. = 6.05, n = 3), and many more subcaudals (75–99, mean = 90.2, s.d. = 4.68, n = 34) than females (ventrals 169–190, mean = 176.3, s.d. = 5.10, n = 44, $t_{s0} = 2.255^*$; subcaudals 68–88, mean = 77.2, s.d. = 4.32, n

= 40, t_{72} = 12.444***). Males similarly have proportionally longer tails than females (TL: males 30.1–40.9% of SVL, mean = 35.2%, n = 33; females 24.4–35.6%, mean = 31.6%, n = 41; U = 1079***). There is no significant sexual dimorphism in SVL (males 167–643 mm, mean = 361.8 mm, s.d. = 137.3, n = 40; females 163–515 mm, mean = 378.5 mm, s.d. = 95.6, n = 44; U = 845.5), although the two largest individuals are male, as are 15 of the 23 individuals with SVL greater than 450 mm.

Nomenclatural history. The Demansia species with the longest nomenclatural history also has the most complex history. The species was described as Lycodon olivaceus by Gray (1842) from material collected by the naturalist John Gilbert from Port Essington. The description was brief, with the useful features confined to coloration: "Dark olive green, in spirits; interspaces between the scales blackish: tail paler: lips and beneath white: scales of the throat olive-edged: the front ventral shields with a transverse central band: cheeks with a dark streak from the back of the eye to the gape" No indication was given of the number of specimens on which the description was based, although Gray (1842: 51) noted that Gilbert's collection was purchased by the British Museum. A series of reptile specimens (BMNH 41.10.13.4-45; Pt Essington, purchased from Gould, Gilbert's employer), corresponding to the reptiles described by Gray (1842), is listed in BMNH registers as containing 13 snakes. Of these 13 specimens, eight are identifiable as belonging to seven of the ten Port Essington snake species listed in Gray's paper. Thus, the remaining five specimens correspond to at least three species, giving at most three syntypes of Lycodon olivaceus. Twenty-six years later, Günther (1858) did not list any Gilbert specimens among



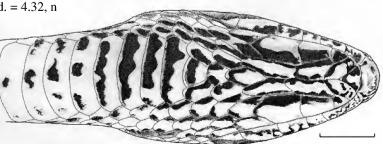


Fig. 8. Head shields and colour pattern of the head and neck of *Demansia olivacea* (AM R107511) in dorsal, right lateral and ventral views. Scale bar = 3 mm.

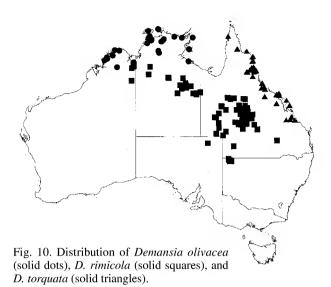


the four British Museum specimens he attributed to this species, although his specimen c. "Adult: bad state. Port Essington" may have been from Gilbert in the absence of any other nominated collector. Günther provided an abbreviated coloration description: "olive-green, skin between the scales black; scales of the sides with two white streaks at the base; a dark streak from the back edge of the eye to the angle of the mouth." This description was repeated by Krefft (1869) as being a condensation of Gray's description. Using this description as a diagnosis, Krefft provided an extended illustrated description of a large Demansia (total length 44 inches) from Port Denison, Queensland, under this name. While he noted that "the few specimens in the [Australian] Museum collection present a variation in colour, sufficiently great to have warranted the creation of a new species", he assumed that they were conspecific with Gray's species. However, the material described and illustrated by Krefft is clearly of the Black Whip Snake Demansia vestigiata, having the anterior ventral scales "sometimes with a sharply defined black margin, which gradually becomes interrupted in the centre", in some examples the ventral scales "uniformly dark (rather bluish) grey, and much lighter anteriorly; in others all the plates are clouded with bluish black, occasionally formed into blotches, and leaving irregular yellowish portions in the middle of each plate", and the anterior dorsal scales "shewing a margin with a black dot at the tip of each scale."

Krefft's description led to a century-long period where the name *Demansia* (or *Diemenia*) *olivacea* was applied to the Black Whipsnake (Shea, 1998). During this period, Macleay (1878) described a new species, *Elapocephalus ornaticeps*, from a single juvenile specimen (formerly Macleay Museum R1305, now AM R31918) from Port Darwin, collected by Edward Spalding, who visited the area between May and September 1877 (Musgrave, 1932). This species was transferred to *Demansia* by Boulenger (1896), and the name was applied to the Marble-headed Whipsnake by subsequent authors (Kinghorn, 1929; Worrell, 1963). Cogger (1967) reexamined the holotype, and was doubtful of the status of the species, suggesting that it may be conspecific with either *D. psammophis* or *D. torquata*. The holotype (Fig. 9) is in good condition, and has 178 ventral scales, 92 subcaudal scales, SVL 186 mm and TL 58 mm. Although the colours have faded, it is still possible to discern the characteristic head and throat pattern of the species.

Cogger & Lindner (1974), working with modern collections from the Port Essington region, recognized that Gray's description most closely fitted the Marble-headed Whipsnake rather than the Black Whipsnake, and returned the name to the correct species, synonymising *D. ornaticeps* with *D. olivacea*, a synonymy with which we agree. In the absence of any type material of the latter species, features of the original description which identify the species and differentiate it from the other whipsnakes in the Top End of the Northern Territory are the olive-edged throat scales, the transverse central marking to the anterior ventrals, and the dark streak from the back of the eye to the angle of the mouth.

Etymology. Gray did not explicitly provide the etymology of the species' name, but it is presumably from the Latin *olivaceus* (olive-coloured), referring to the "dark olive-green" coloration mentioned in the description. The etymology of *ornaticeps* is presumably from the Latin *ornatus* (adorned, decorated) and *-ceps* (head), alluding to the characteristic marbled head of this taxon.



Distribution. Extreme north of Kimberley and Top End of the Northern Territory. Kimberley records from 18 km E Kuri Bay in the west to the Kununurra region in the east. Northern Territory records from "Wangi" Stn and the Darwin area in the west to "Bing Bong" Stn in the east, and including Melville I. and Groote Eylandt (Fig. 10).

Geographic variation. The four specimens from the Kununurra region (WAM R81412, R127315, R113398, R119535) include the largest three specimens (SVL 643, 584, 557 mm respectively for the former three; next largest from other localities 518 mm) and have four of the highest five ventral counts (196, 195, 185, 196 respectively, only one other count (190) higher than 185). When these four individuals are excluded, there are no significant relationships among males between longitude and either number of ventral scales ($r^2 = 0.060$, n = 36; $F_{1,34} = 2.160$), subcaudal scales ($r^2 = 0.004$, n = 32; $F_{1,30} = 0.117$), SVL ($r^2 = 0.144$, n = 37; $F_{1,35} = 0.744$) or relative tail length (r² = 0.044, n = 31; F_{1,29}) = 1.329), nor are there any significant relationships among females between longitude and SVL ($r^2 = 0.011$, n = 43; $F_{1.41}$ = 0.457). However, there are significant relationships among females between longitude and number of ventral scales $(r^2 = 0.228, n = 43; F_{1,41} = 12.083^{**}; ventrals = 278.448 - 0.776^{*}longitude), subcaudal scales (r^2 = 0.193, n = 39; F_{1,37} = 0.193, n = 100, n = 100,$ 8.837^{**} ; subcaudals = 0.630^{*1} longitude - 6.011) and relative tail length ($r^2 = 0.209$, n = 40; $F_{1,38} = 10.039^{**}$; TL/SVL = 0.004*longitude -0.214). Plots of these variables against longitude suggest that there is a smoothly clinal decrease in ventral scales and a smoothly clinal increase in relative tail length with increasing longitude, but that the variation in number of subcaudals at least partly reflects a narrowed range of variation for western material within the lower end of the range of variation of other populations.

Comparison with other species. *Demansia olivacea* shows two rare character states in the genus: a median series of dark spots on the anterior ventrals, and absence or near absence of pale pre- and postocular bars (the former unique, the latter shared with *D. simplex* and most black whip snakes). It may be differentiated from *D. angusticeps*, with which it was previously considered conspecific, in the two coloration features above, and in the characteristically finely mottled

greyish lips, absence or near absence of a brown transrostral streak, and generally lower scale counts. The two species are allopatric, although they approach to within 55 km (Old "Theda" *vs* Kalumburu).

Demansia olivacea differs from both *D. calodera* and *D. flagellatio* in lacking a dark collar, as well as in the two coloration characteristics listed above. It is allopatric to both species. For comparison with other species, see subsequent accounts.

Specimens examined. AM R8252, R31918, R31936, BMNH 84.9.13.22, QM J2229, J2980, SAM R6645a-e, Pt Darwin, NT; AM R10215, R25779, BMNH 1926.2.25.100-102, Groote Eylandt, NT; AM R12382, Yirrkala, NT; R12847, R12881, Humpty Doo, NT; R13649, Cape Arnhem, NT; R14031, MV 60344-47, D8485, D8567-68, D8596-97, NTM R21108, R5970, R21125, R32366, SAM R2179, WAM R40834, Darwin, NT; AM R20246, Edith River, NT; R26276-77, R26280, R76956-58, R77368, R89098, R95585-86, Angurugu Mission, Groote Eylandt, NT; R29998, R30095, R30100, Port Essington, NT; R30093, "Black Point" HS, Port Essington, NT; R30094, R30096-99, Black Point, Port Essington; R39099, Melville I., NT; R88830, Jabiluka project area, NT; R107510, Black Point Bore, Port Essington, NT; R107511, Black Point Swamp, Port Essington, NT; R119378, WAM R77021, Mitchell Plateau, WA; AM R133327, Donydji, NT; BMNH 51.10.25.6, Australia; 1946.1.18.40, 1946.1.18.45, NW Australia; MV R12812-14, NT; D4691, South Australia (in error); MV DT-D118, nr Cape Arnhem, NT; NTM R103, Katherine Farms Rd, Katherine, NT; R355, Berry Springs Reserve, NT; R885, McMillans Rd, Darwin, NT; R920, Rapid Creek, Darwin; R1050, WAM R47589, Casuarina, Darwin, NT; NTM R3405, Howard Springs, NT; R4706, Gunn Pt, nr Darwin, NT; R7587, Florence Falls, "Wangi" Stn, NT; R8182, 17-mile, Darwin, NT; R13376, Cooinda, NT; R13377, Kakadu NP, NT; R16139, Cadell River crossing, NT; R17068, Palmerston, NT; R17188, SAM R29956, Humpty Doo district, NT; NTM R32364, USNM 128263, Nightcliff, Darwin, NT; NTM R32365, The Narrows, Darwin, NT; R32368, "Bing Bong" Stn, NT; USNM 128448, Umba Kumba, Groote Eylandt, NT; WAM R955-56, R1575, Drysdale River, WA; R13649, Kalumburu, WA; R23287, 35 mi. SE Darwin, NT; R29687, Mitchell Plateau, between Mitchell and Lawley Rivers, WA; R40419, 11 mi. E Kuri Bay, WA; R44007, Careening Bay, nr Pt Nelson, WA; R73644, "Gibb River" HS, WA; R81412, R113398, Kununurra, WA; R99118, 10 km NW September Point, Cape Bougainville, WA; R99246, Mt Trafalgar, WA; R119535, R127315, Mirima NP, WA

Demansia quaesitor n.sp. Shea

Figs. 11-12

Type material. HOLOTYPE NTM R16836, "Hodgson Downs", Mt Langdon, NT, collected by J. Woinarski on 29.v.1991. PARATYPES. AM R13047, Katherine, NT; R28248, Calvert River, NT; R64322, Bralmana River, Arnhem Bay, NT; R119388, "6 km along Brandy Ck rd, 10 km W Airlie Beach, Qld" (possibly in error for Cannon Hill, NT); MV D10059–64, Roper River Mission, NT; NTM R929, "Hartley's Ck, Qld" (in error); R2075, 5 mi. ENE "Victoria River Downs" HS, NT; R5623, Wave Hill, NT; R20542, R20547, R20611, Cape Crawford area, NT; R20570, Moonlight Gorge, NT; QM J47791, "Bowthorn" Stn, Qld; WAM R31054, "Kildurk", NT; R55900, junction of Ord and Behn Rivers, WA; R86456, 12 km W Mt Evelyn, WA; R86457, Smoke Ck, WA; R103178, R103181, Bungle Bungle NP, WA.

Diagnosis. A small (maximum SVL 565 mm) *Demansia* with head blue-grey to orange-brown, paler than body, dark transrostral streak (when distinct) reaching orbit, dark postocular teardrop marking extending across top of fifth supralabial and middle of sixth supralabial, directed towards and often reaching ventral extremity of a narrow dark collar on nape, and dark facial and nape markings not or only weakly and diffusely pale-edged.



Fig. 11. Holotype of Demansia quaesitor (NTM R16836).

Description. Based only on type series; see below for comparative data on other populations tentatively assigned to this species.

Head dorsum pale blue-grey to orange-brown, with variable expression of dark blotches and flecks (the former over parietals and temporals, the latter on snout); a darker brown transrostral streak usually distinguishable, not or only faintly pale-margined, extending to orbit, occasionally with fine ventral extensions along sutures between supralabial scales; labials below this marking pale grey to brown, very finely marbled; a brown teardrop marking posterior and slightly ventral to eye, from anteroventral corner of lower postocular and posterodorsal corner of fourth supralabial, across dorsal third of fifth supralabial, ventral third of temporolabial and lower third of sixth supralabial, from where it may extend further posteriorly to reach the anteroventral corner of dark nape band; dark teardrop not or only weakly and narrowly pale-margined; usually (very obscure in largest adults) a dark grey nuchal band, about 3-4 scale rows wide, across sides and dorsum of nape, its anterior margin 1–3 scale rows posterior to parietals; this band at most very weakly, diffusely and narrowly pale-edged.

Body dorsum grey-brown (occasionally, in very large individuals, almost black), darker than head, often more brown or yellow caudally on body and tail; neck ventrolaterally with dark spots centrally in scales posterior to dark nape band.

Venter pale, immaculate or throat with a few weak darker flecks or macules.

Dorsal colour extends ventrally onto lateral extremity of ventral scales.

Colour notes on one specimen (WAM R86457, L. Smith, pers. comm.) indicate that the top of the head was coppery brown with dark brown flecks, the margins of the head shields dark reddish brown. The dark nuchal bar was blackish-brown, the dark markings on chin and throat black. Body dorsum was greenish-yellow, freckled grey, with individual dorsal scales having a central charcoal mark, and the posterior part of the scale having a reddish-brown subterminal zone. The belly was pale yellow. The mouth was pinkish white, the tongue black tipped white, and the iris orange-brown smudged black, with a narrow orange ring around the pupillary margin, and the dorsal part pale.

Ventrals 182–195 (mean = 189.3, s.d. = 3.66, n = 25); subcaudals 69–99 (mean = 87.9, s.d. = 7.40, n = 22). SVL 154–565 mm (mean = 361.5 mm, s.d. = 143.1 mm, n = 25); TL 25.7–37.7% of SVL (mean = 32.2%, s.d. = 3.0%, n = 22).

Sexual dimorphism. Males have significantly greater numbers of subcaudal scales (86–99, mean = 92.1, s.d. = 4.34, n = 14) than females (69–87, mean = 79.5, s.d. = 5.92, n = 6; $t_{18} = 5.331^{***}$) and have longer tails (TL: males: 30.1–37.7% of SVL, mean = 33.7%, n = 14; females: 25.7–33.3%, mean = 29.8%, n = 6; U = 71*), but are generally smaller than females (SVL: males: 154–563 mm, mean = 328.6 mm, s.d. = 136.4, n = 14; females: 200–565 mm, mean = 449.8 mm, s.d. = 116.4, n = 9; U = 30*). Number of ventral scales is similar, and not significantly different, between males (182–193, mean = 188.5, s.d. = 3.42, n = 14) and females (182–195, mean = 189.8, s.d. = 4.09, n = 9; t_{21} = -0.812).

Nomenclatural history and description of holotype. Material of this species has previously been referred to *D. olivacea* (Storr, 1978; Gambold, 1992; McKenzie *et al.*, 1995; Stammer, 1976; Storr *et al.*, 1986; Cogger, 1996, the latter three publications including photographs), despite the presence of a dark collar in most instances.

The male holotype (Fig. 11–12) has 192 ventrals, 96 subcaudals, snout-vent length 469 mm and tail length 177 mm.

Etymology. From the Latin noun *quaesitor*: a judge of the criminal court, alluding to the generally sombre appearance of the species, which lacks pale markings to the dark collar, and has a pale head; a secondary meaning (a searcher or seeker) alludes to the foraging ecology of the genus.

Distribution. From the east Kimberley, through Arnhem Land, and east to at least "Bowthorn" Stn, Qld. Tentatively associated with this species are two additional peripheral populations: Koolan I. in the west Kimberley, and northwestern Qld, southeast of the main distribution, from Camooweal and Doomadgee, SE to 52 km W of "Vergemont" Stn (Fig. 13).

Two records from coastal east Queensland (AM R119388, NTM R929) are presumed to be in error. Both records are distant from other localities and within the range of *D. torquata*, which similarly possesses a dark nape collar. Both were presented via persons keeping large collections of live snakes, raising the possibility that they were confused with true *D. torquata* in those collections. The former specimen additionally has the same locality data as a specimen of *D. torquata* (AM R119465) from the same source but registered on a different date. It is possible that R119388 is an otherwise missing *Demansia* from that collection with locality Cannon Hill, NT.

Geographic variation. Within the main body of the distribution, head colour changes gradually from bluish in the east to more orange in the west, with a concurrent decrease in expression of dark markings on the head dorsum. Further, the dark nape band is narrower in the west, its anterior margin lying further posterior to the parietals.

The Koolan I. population is similar in scalation and coloration to material from the east Kimberley. The six specimens have 184–194 ventrals, 74–86 subcaudals, SVL 494–566 mm and tail length 26.7–30.6% of SVL. The body dorsum is relatively dark, and the nape band is consequently not as pronounced as in the main part of the distribution.

In the northwestern Queensland population, the nape band is absent, except in small juveniles, which usually show traces of it laterally. Further, there is variation in the position of the dark teardrop marking. In some individuals, apparently due to loss of the upper margin, the dark teardrop marking resembles that of D. angusticeps, a resemblance heightened by greater development of pale edges to the teardrop, reduction in the posterior extension of the dark transrostral streak to the orbit, coarser marbling of the anterior supralabials, and a more strongly variegated and spotted gular region. The live individual illustrated by Cogger (1996, as D. olivacea) also shows some resemblance to D. angusticeps in possessing a more orange head than in other eastern D. quaesitor. Scalation of the Queensland population (ventrals 185-198, n = 13; subcaudals 73-95, n = 12) resembles that of other D. quaesitor. Relative tail length is similar (27.5–35.8% of SVL, n = 12), as is SVL, although the largest individual (AM R15600, 584 mm) is a little larger than the largest typical *D. quaesitor*. A typically patterned *D. quaesitor* adult with obvious dark nape band is available from "Bowthorn" Station (QM J47791), only 56 km WSW from Doomadgee, and 68 km NNW from "Adel's Grove", from where the Queensland population is known. Althouth this form is tentatively assigned to *D. quaesitor*, it is possible that it represents an eastern isolate of *D. angusticeps*, or a distinct species.

Within the range of typical *D. quaesitor*, there is no relationship between longitude and number of ventral scales ($r^2 < 0.001$, n = 28; $F_{1,26} = 0.006$), nor is there any relationship for females between longitude and number of subcaudals ($r^2 = 0.169$, n = 8; $F_{1,7} = 1.224$), SVL ($r^2 = 0.062$, n = 11; $F_{1,9} = 0.598$) or relative tail length ($r^2 = 0.134$, n = 8; $F_{1,6} = 0.929$). For males, although there is no relationship of longitude with SVL ($r^2 = 0.142$, n = 16; $F_{1,14} = 2.325$), there is a positive relationship with both number of subcaudal scales ($r^2 = 0.297$, n = 16; $F_{1,14} = 5.912*$; subcaudals = 0.579*longitude + 15.226) and relative tail length ($r^2 = 0.254$, n = 16; $F_{1,14} = 4.774*$; TL/SVL = 0.002*longitude + 0.042).

Comparison with other species. *Demansia quaesitor* is the only *Demansia* possessing a well-developed dark nuchal band but lacking pale edges to this band. Apart from the presence of a nuchal band, it is most similar to *D. angusticeps*, with which is overlaps in the east Kimberley (both species have been recorded from 12 km W "Mt Evelyn"). It additionally differs from *D. calodera*, with which it shares a dark nape band, in having more numerous ventral scales (182–195, mean 189.3 vs 171–189, mean

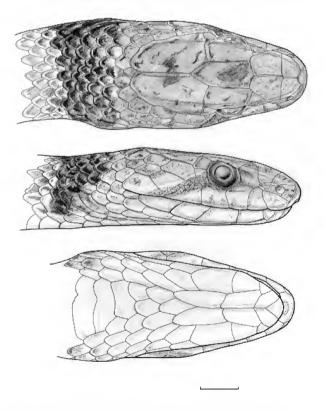


Fig. 12. Head shields and colour pattern of the head and neck of the holotype of *Demansia quaesitor* in dorsal, right lateral and ventral views. Scale bar = 3 mm.

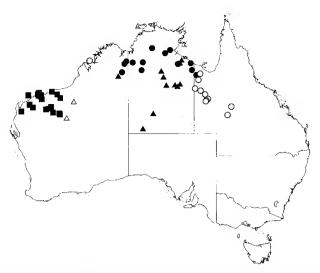


Fig. 13. Distribution of *Demansia quaesitor* (typical population: solid circles; peripheral populations tentatively assigned to this species: open circles), *D. rufescens* (solid squares), and *D. shinei* (type series: solid triangles; referred specimens, open triangles)

180.4), and subcaudal scales (male means 92.1 vs 78.2; female means 79.5 vs 71.1). The two species are allopatric and unlikely to be confused. It additionally differs from D. flagellatio, which has bold broad pale edges to its dark nuchal band, in having markedly fewer ventral and subcaudal scales. Typical D. quaesitor approaches to within 112 km of D. flagellatio ("Bowthorn" vs "Riversleigh"), and the latter species is sympatric around Mt Isa with the inornate Queensland population assigned to D. quaesitor (Stammer, 1976). Demansia quaesitor geographically overlaps with D. olivacea in the Katherine area and in eastern Arnhem Land; the two species are readily differentiated by the facial and nape markings, and D. quaesitor has generally higher ventral counts than D. olivacea (male means 188.5 vs 179.0; female means 189.8 vs 176.3). For further comparisons with other species, see subsequent accounts.

Additional specimens examined. Koolan I. Population. WAM R28071, R47684, R82993, R83863, R83967, R103730, Koolan I.

Northwestern Qld Population. AM R11337, nr Duchess; R15600, R25986, R28261, Mt Isa; R26596, R64709, Mt Isa district; R72763, 168 km N Boulia on Mt Isa rd; R73041, 8 km N Dajarra; R119379–80, Camooweal tip; R162274, Adel's Grove, Riversleigh; QM J39472, Winton area; J43221, 75 km NW Mt Isa, nr Buckley River crossing; J52510, opal mine, 52 km W of "Vergemont" Stn; R52726, Century Project site, "Lawn Hill" Stn; SAM R6192, Doomadgee.

Demansia rimicola n.sp. Scanlon

Figs. 14–15

Type material. HOLOTYPE AM R62257, 61.4 km N Muttaburra via Hughenden Hwy, Qld (22°10'S 144°15'E), collected by A. Greer, E. Cameron, H. Cogger, R. Sadlier & P. Webber on 17.vii.1977. PARATYPES. All other 166 specimens listed as examined. **Diagnosis**. A moderately large, stout *Demansia* (SVL up to 740 mm) with a dark, pale-edged collar on nape (often indistinct in adults, with the pale edges persisting the longest), dark spots on head dorsum, pale postocular bar separated from ventral coloration by an isthmus between dark head and dark teardrop marking, and constricted to give the appearance of two pale confluent blobs, and two posteriorly diverging rows of dark spots on anterior ventrals.

Description. Head dorsum and nape mid-brown, usually with darker brown flecks and spots, often aligned along sutures, but otherwise without a restriction to region, and often some fine pale vermiculations on snout; an obscure, slightly darker brown transrostral streak, often absent centrally, usually at least weakly cream edged above and below, not reaching orbit, but angled posteroventrally along suture between second and third supralabials; a midbrown teardrop marking, usually with dark brown margins, posteroventral to eye, from ventral half of lower postocular and usually at least posterodorsal corner of fourth supralabial, across dorsal half of fifth supralabial, ventral third of temporolabial, and most of sixth supralabial, where it joins the dorsal head coloration; a prominent cream preocular bar, extending posteroventral to edge the dark teardrop anteriorly; a cream postocular bar covering anterior half of upper postocular, dorsal half of lower postocular, anterior third of primary temporal and central third of temporolabial, constricted where it crosses sutures by brown margins, giving the appearance of a reduction to a pair of pale blobs on the side of the face; an obscure undulating narrow (1-2 scale wide) pale nuchal band, most prominent laterally, partially or completely separating head dorsum from nape over first two dorsal scale series; brown nape band terminates caudally in a weakly defined oblique pale bar, directed posteroventrally on sides of neck; both pale nuchal markings continuous, or nearly so, with ventral coloration.

Body dorsum mid-brown to mid yellow-brown, pigment on lateral scale rows often concentrated centrally to give a series of broad dark and narrow pale stripes along sides.

Venter yellow, throat strongly marbled with dark brown, including stripes along suture between genials and infralabials, continuous with a series of dark brown macules on anterior ventrals, aligned to form a paired row of spots, diverging and dissipating posteriorly along lateral extremities of ventrals.

Dorsal ground colour blends with ventral ground colour on lateral extremities of ventrals.

Three recently collected individuals from Sturt National Park in NSW (AM R158425, R158876, R158930), and a freshly dead individual from north of Winton on the Hughenden rd, Qld (22°10.108'S 143°05.272'E; colour photograph from M. Anthony) had the body venter bright orange-red in life.

Ventrals 178–203, mean = 190.2, s.d. = 3.93, n = 145; subcaudals 68–96, mean = 83.4, s.d. = 5.38, n = 127. SVL 155–740 mm, mean = 488.1 mm, s.d. = 120.5 mm, n = 152; TL 25.4–41.5% of SVL (mean = 31.8%, s.d. = 2.4, n = 127).

Sexual dimorphism. Males have significantly greater numbers of subcaudal scales (73–93, mean = 85.9, s.d. = 4.71, n = 50) than females (68–89, mean = 80.5, s.d. = 4.313, n = 58; $t_{106} = 6.259^{***}$) and have longer tails



(TL: males: 28.2–41.5% of SVL, mean = 33.0%, n = 50; females: 27.9–33.8% of SVL, mean = 30.9%, n = 57; U = 2195.5***). Males are not significantly different to females in SVL, although the difference is nearly significant (SVL: males: 248–719 mm, mean = 528.1 mm, n = 59; females: 229–740 mm, mean = 496.2 mm, n = 69; U = 2426, p = 0.062). Mean number of ventral scales is not significantly different between males (178–197, mean = 190.0, s.d. = 3.77, n = 57) and females (182–203, mean = 190.2; s.d. = 4.12, n = 66; $t_{121} = -0.226$).

Nomenclatural history and description of holotype. *Demansia rimicola* has previously been illustrated in Shine (1980), Swan (1990, 1995), Healey (1997), Swan *et al.* (2004) and Wilson & Knowles (1988), identified as *D. torquata* in the former five cases and as an unidentified *Demansia* in the latter.

The holotype (Figs. 14–15), an adult male, has 193 ventrals, 92 subcaudals, SVL 597 mm and TL 207 mm.

Etymology. From Latin noun *rima* (a crack) and verb *colo* (to inhabit), meaning "crack-dweller", alluding to the association of this species with cracking clay soils.

Distribution. Cracking clay soils of northern central Australia, from the southeast Kimberley (Smoke Creek, "Flora Valley"), south-east to Goyder's Lagoon, SA and the Tibooburra region, NSW, east to Bindango Siding, Qld, and north-east to the Hughenden district, Qld (Fig. 10). A single record (QM J13447) from Rollingstone, north of Townsville on the Queensland coast, is considered erroneous due to its distance from other localities and the very different habitat at this locality.

Geographic variation. With sexes pooled, there is a slight but significant positive correlation between number of ventral scales and longitude ($r^2 = 0.069$, n = 137; $F_{1,135} = 9.929^{**}$), with the relationship expressed as ventrals = 0.274^* decimal longitude + 151.398. Examination of the plot of these two variables suggests that this is largely due to western populations having reduced variation in comparison to eastern populations; while western values are generally low, they are fully within the range of variation of eastern populations. There is no significant relationship between SVL and longitude ($r^2 = 0.003$, n = 144; $F_{1,142} = 0.448$).

Because of the significant sexual dimorphism in number of subcaudals and relative tail length, sexes were analysed separately for geographic variation. There is no significant relationship between number of subcaudals and longitude for either males ($r^2 = 0.050$, n = 48; $F_{1,46} = 2.398$) or females (r^2 = 0.006, n = 53; $F_{1,53} = 0.329$). However, there is a significant positive relationship between relative tail length and longitude for both males ($r^2 = 0.146$, n = 48; $F_{1,46} = 7.838**$; relative tail length = 0.003*longitude - 0.061) and females ($r^2 = 0.089$, n = 52; $F_{1,52} = 4.873*$; relative tail length = 0.001*longitude + 0.140). As with number of ventral scales, a plot of the two variables suggests that the relationship is largely due to reduced variation among western material, with the range of variation in the east fully encompassing the generally low values in the west.

In the east of the distribution, *D. rimicola* spans a wide latitudinal range. When only specimens from east of the level of the Queensland border (138°E) were analysed, there was no significant relationship between SVL and latitude ($r^2 = 0.001$, n = 121; $F_{1,119} = 0.089$), nor between number of ventral scales and latitude, although the latter approached significance ($r^2 = 0.030$, n = 114; $F_{1,112} = 3.483$,

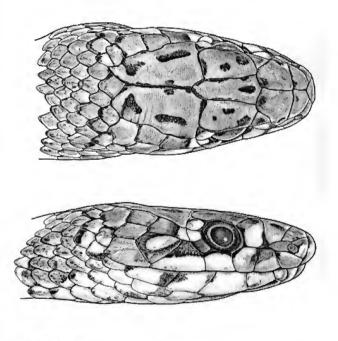
p = 0.065). With sexes separated, there were no significant relationships between relative tail length and latitude (males: $r^2 = 0.029$, n = 41; $F_{1,39} = 1.169$; females: $r^2 = 0.003$, n = 43; $F_{1,41} = 0.117$), or, for females, between subcaudals and latitude ($r^2 = 0.005$, n = 44; $F_{1,42} = 0.207$). However, there was a significant negative relationship between number of subcaudals and latitude in males ($r^2 = 0.113$, n = 41; $F_{1,39} = 4.957$ *; subcaudals = 103.502 - 0.739*latitude). Examination of a plot of the two variables suggests that the relationship is largely due to the four males in the extreme south having values in the lower half of the range of variation of more northern individuals.

Comparison with other species. Demansia rimicola differs from all other species in the nature of the head markings, particularly the reduction (in extent, but not intensity) of the pale postocular bar, which does not reach the venter or the pale anterior nuchal band, and is constricted and sharply angulated, and the presence of two diverging rows of prominent dark spots on the anterior ventrals. It is further differentiated from D. angusticeps and D. olivacea in having a broad dark nape band (contrast usually lost in adults) edged with cream, from D. calodera in its much greater size and presence of dark spots on the head dorsum, from D. flagellatio in its greater size and more robust build, absence of a second dark nuchal band and generally paler and less contrasting head pattern, and from D. quaesitor in its greater size and more sharply-defined and prominent pale postocular markings. The distribution of D. rimicola overlaps with D. angusticeps in the east Kimberley (Granny Soak, 12 km W "Mt Evelyn" and 6 km 200° Turkey Creek vs Smoke Creek, Flora Valley, Argyle Lagoon and 6 km W Old "Argyle Downs"), although sympatry between the two species is not yet known. It is sympatric with D. quaesitor at Smoke Creek. It is geographically distant to D. calodera, D. flagellatio and D. olivacea. For comparison with other species, see subsequent accounts.

Specimens examined. AM R6536–37, "Sylvania", nr Hughenden, Qld; R8976, R9109, nr Hughenden, Qld; R10121, Nappapirra, Cooper's Ck, Qld; R13011, Hughenden, Qld; R16941, R105954, SAM R20348, Tibooburra, NSW; AM R19282, central west Qld; R40504, 3 mi. W "Rodney Downs", Qld; R40505, 9 mi. SE "Rodney Downs", Qld; R58582, Blackall, Qld; R62257, 61.4 km N Muttaburra via Hughenden Hwy, Qld; R73549, R74513, Maxwelton, Flinders Hwy, Qld; R92721, 5 km S "Olive Downs" HS, NSW; R105955, ANWC R2718, "Mt King", Tibooburra, NSW; AM R111330, No. 2 Bore, "Davenport Downs", Qld; R114134, Winton district, Qld; R141726, Elliot, NT; R142965, 39 km N Longreach, Qld; R143072, "Cannington" Stn, S of McKinlay, Qld; R158425, 8km N "Mt Wood" HS on Gorge Loop Rd, Sturt NP, NSW; R158876, Twelve

Mile Ck crossing on Silver City Hwy, Sturt NP, NSW; R158930, Kings Ck crossing, Gorge Loop Rd, Sturt NP, NSW; ANWC R797, 31 mi. SE Boulia on Coorabulka rd, Qld; R830, "Lorna Downs" Stn, SE Boulia, Qld; R4510, Stubblefield Tank, Sturt National Park, NSW; BMNH 1906.3.31.16, 1906.5.26.3, NTM R32389, "Alexandria", NT; MV R11342, D2822, Qld; NTM R2076, "Pidgeon Hole" outstation, "Victoria River Downs", NT; R3642, "Brunette Downs" HS, NT; R3667-68, "Anthony's Lagoon" HS, NT; R6444, R8840, Frewena, NT; R6808, Wave Hill, NT; R9690, 19°18'S 136°04'E, NT; R9751, Avon Downs Police Station, NT; R14017, 17°56'S 133°37'E, NT; R16777-78, "Rockhampton Downs" airstrip, NT; R32363, R32390-91 "Avon Downs", NT; R32387, Qld Border, Barkly,

NT; QM J1587-89, no locality; J2276, Corfield, Qld; J2745, Tangorin, N of Longreach, Old; J5321, J5337, J5397, Julia Creek, Old; J5396, Julia Creek district. Old; J5458, "Garomna", Julia Creek, Qld; J6149, "Ruthven", SW of Isisford, Old; J6237, Isisford district, Old; J6581, Bindango Siding, via Roma, Qld; R9763, "Balmoral", Ilfracombe, Qld; J12324, Muttaburra, Qld; J13447, "Rollingstone, N of Townsville, Qld" [in error]; J13588, "Corunna", via Corfield, Qld; J21029, "Ingleside", via Longreach, Qld; J23305, J23679, J24026, J24044, "Maranthona" Stn, 72 km N Longreach, Qld; J23307, "Rosebank" Stn, 9.6 km S Longreach, Qld; J23308, Middleton Hotel, 176 km SW Winton, Qld; J23650, J26937, J27594, J34117, Winton, Qld; J24292-96, J24572, J25385, J28412-15, "Proa" Stn, via Nelia, Old; J26035, "Beryl" Stn, via Longreach, Qld; J26333, nr channels of the Western River, Winton, Qld; J27508, J54613, SAM R4060, Ilfracombe, Qld; QM J33548, nr "Bundeema" HS, "Kihee" Stn, 128 km W Thargomindah, Qld; J35568, Morney Plain, Qld; J37155, 22 km S Longreach, Qld; J39317, c.70 km E Boulia on Winton rd, Old; J41386, J43763-66, J43770, J49861, J50013, J52527, J54615, Longreach, Qld; J41388-90, Longreach area, Qld; J41849, "Monkira" Stn, Diamantina Shire, Qld; J47936, Aramac, Qld; J49798, "Bimerah" Stn, 100 km S Longreach, Qld; J49868, 6 km S Longreach, Qld; J49872, J49877, Longreach area, Qld; J49873, J49875, "Weeumbah", 80 km S Longreach, Qld; J49964, "Denton" Stn, 90 km NW Longreach, Qld; J49965, Gull St, Longreach, Qld; J49991, nr "Bexley" HS, Qld; J49996, nr homestead turnoff on main rd, "Rosebank" Stn, Qld; J49998, 45 km S Longreach on Jundah rd, Old; J50000, nr homestead turnoff, "Ban Ban' Stn, Longreach-Jundah rd, Qld; J50004, 6 km S Longreach on Arrilalah rd, Qld; J50006, "Cork" Stn to Winton rd, Qld; J50011, Arrilalah rd, 300 m S Longreach-Jundah rd, Qld; J50030, Arrilalah rd, nr "Weeumbah" shearing shed, Qld; J50032, "Depot Glen" Stn, 13 km NE Stonehenge, Qld; J50033, W side of Mungerie Ck, Ski rd, Qld; J51141, J51144, nr "Durrie" HS, Qld; J51244, J57207, "Bellen Park" Stn, Longreach to Jundah rd, Qld; J51252, nr station turnoff, "Waroona" Stn, Qld; J51268, 5 km S "Glen



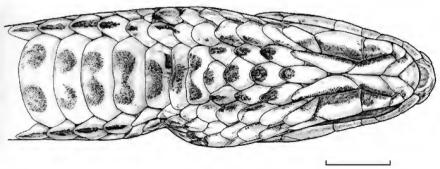


Fig. 15. Head shields and colour pattern of the head and neck of holotype of *Demansia rimicola* in dorsal, right lateral and ventral views. Scale bar = 5 mm.

Thomson" Stn turnoff, Qld; J51511, "Rosebark [sic]" Stn, via Longreach, Old; J51526, "Cotswold Hills", 40 km WSW Winton, Old; J52499, J52509, J54278, "Yarawa" HS, 60 km ESE Stonehenge, Qld; J52503, nr "Laidlaw" HS, Qld; J52505, nr turnoff to "Fernhurst", Longreach-Jundah rd, Qld; J52508, "Westerton" HS, Qld; J52516, J52521, "Bellen Park" HS, Qld; J52520, Arrilalah rd, nr "Rosabel" turnoff, Qld; J52859, Boree Ck, 32 km S "Brunette Downs" Stn, NT; J54276, 15 Cassowary St, Longreach, Qld; J54277, Stonehenge Pub, Qld; J58658, BHP study site, "Cannington" Stn, Qld; J58667, adjacent to "Cannington" camp, Qld; J58668, Borefield, Qld; J58838, Morella, Qld; J59912, Jundah rd, Longreach, Qld; J59916, on hwy between Ilfracombe and Barcaldine, Qld; J60275, "Durrie" Stn, Qld; SAM R4727, "Planet" HS, Qld; R15471, "Minnie Downs", Qld; R19851, 26 km N "Clifton Hills" Stn, Goyder's Lagoon, SA; R34263, "Soudan" HS, NT; WAM R42809, 4 mi. W old "Argyle Downs" HS, WA; R55901, Argyle Lagoon, Ord River, WA; R86887, "Flora Valley", WA; R89986, Smoke Creek, WA.

Demansia rufescens Storr, 1978

Figs. 16–17

Demansia olivacea rufescens Storr, 1978: 292. Holotype: WAM R52747, Marandoo minesite, near Mt Bruce, WA.

Diagnosis. A small *Demansia* (maximum SVL 511 mm), lacking a dark collar on the nape or dark markings on the anterior ventrals, and with prominent transrostral, preocular and postocular markings and a reddish dorsum.

Description. Head dorsum dark brown to red-brown, snout sometimes weakly marbled with paler brown vermiculations; a narrow dark brown transrostral streak, extending narrowly posteriorly to reach orbit, and usually with extensions along sutures between first three supralabials, weakly creamedged above and below; anterior supralabial scales cream with dark brown macules centrally (macules sometimes enlarged to obliterate cream elements); dark brown teardrop marking posteroventral to eye, beginning on ventral half of lower postocular and (variably) posterodorsal corner of fourth supralabial, across ventral corner of primary temporal, dorsal to posterodorsal third of fifth supralabial, anteroventral third of temporolabial, and across anteroventral third of sixth supralabial and (variably) last two (6/7) infralabials, extending obscurely posteriorly along second and third scale rows on neck; cream preocular bar, usually continuous with the pale edges to dark transrostral streak, and interrupted by orbital extension of that dark streak, continuing posteroventrally to edge dark teardrop anteriorly (occasionally, in individuals with extensively dark anterior supralabials, the continuity is broken); cream postocular bar over ventral half of upper postocular, dorsal half of lower postocular, anteroventral third of primary temporal, across centre of temporolabial and sixth supralabial, then continuing along side of neck, dissipating along scale rows 4–5.

Body dorsum olive red-brown, extending ventrally to scale row 1, before blending gradually with ventral ground colour.

Ventral ground pale yellowish to cream; throat occasionally with very obscure pale brown streaks along genial/ infralabial suture.

Ventrals 176–200, mean = 190.4, s.d. = 6.42, n = 31; subcaudals 65–85, mean = 74.4, s.d. = 5.29, n = 29. SVL 160–511 mm, mean = 337.0 mm, s.d. = 107.8 mm, n = 32; TL 23.6–32.4% of SVL (mean = 27.5%, s.d. = 2.0, n = 30). **Sexual dimorphism**. Males have significantly greater numbers of subcaudal scales than females (65–85, mean = 76.8, s.d. = 5.91, n = 12 *vs* 65–77, mean = 71.1, s.d. = 3.60, n = 8; $t_{18} = 2.399^*$). There are no significant differences between males and females in number of ventral scales (males: 180–199, mean = 190.0, s.d. = 6.08, n = 12; females: 182–200, mean = 190.1, s.d. = 6.49, n = 10; $t_{20} = -0.037$), SVL (males: 184–446 mm, mean = 341.7 mm, s.d. = 102.0, n = 12; females: 299–502 mm, mean = 393.2, s.d. = 64.2, n = 10; U = 45.0) or TL (males: 24.0–32.4% of SVL, mean = 28.0%, n = 12; females: 24.7–29.8%, mean = 27.7%, n = 8; U = 60.0).

Nomenclatural history and description of holotype. *Demansia rufescens* was described, as a subspecies of *D. olivacea*, from a series of 13 Pilbara specimens by Storr (1978). It was subsequently listed as a full species by Storr & Harold (1985), without comment, although the only diagnostic character cited as separating it from *D. olivacea (sensu* Storr, 1978, who included specimens of *D. angusticeps, D. rimicola, D. shinei* and *D. papuensis* in his concept) was the reddish dorsum.

The female holotype (Figs. 16–17) has ventrals 200, subcaudals 72, SVL 448 mm, tail length 125 mm.

Etymology. The name is derived from the Latin adjective *rufescens* (becoming red), alluding to the dorsal coloration of this taxon (Storr *et al.*, 1986).

Distribution. Pilbara region of Western Australia, from "Marilla" in the south-east to Pt Hedland, "De Grey River" Stn and Marble Bar in the northeast, and including Hermite, Dolphin and Barrow Islands (Fig. 13).

Geographic variation. There is no longitudinal variation in SVL ($r^2 = 0.004$, n = 32; $F_{1,30} = 0.132$), or relative tail length ($r^2 > 0.001$, n = 30; $F_{1,28} = 0.002$). The relationship between number of ventral scales and longitude approaches significance (number of ventral scales = 1.533*longitude + 10.584) ($r^2 = 0.120$, n = 31; $F_{1,20} = 3.966$, p = 0.056).

10.584) ($r^2 = 0.120$, n = 31; $F_{1,29} = 3.966$, p = 0.056). For males, there is a significant longitudinal variation in number of subcaudal scales ($r^2 = 0.372$, n = 12; $F_{1,10} = 5.917^*$; subcaudals = 2.070*longitude - 165.986). The pattern of change is evenly clinal, with higher values in the east. However, females do not show the same pattern, with no significant longitudinal variation in subcaudal scales, or even a trend towards such a pattern ($r^2 = 0.001$, n = 8; $F_{1,6} = 0.008$).

Comparison with other species. *Demansia rufescens* is most similar to *D. angusticeps*, which which it shares the absence of a nuchal band. The two species are similar in facial colour pattern and number of ventral scales, but differ in the greenish dorsum of *D. angusticeps* compared to the reddish dorsum of *D. rufescens*, and generally lower subcaudal counts for *D. rufescens* (males: 65–85, mean 76.8 vs 80–98, mean 91.1; females: 65–77, mean 71.1 vs 74–91, mean 81.1). The two taxa approach to within about 170 km ("De Grey River" vs 325 km S Broome), and it is possible that they are even closer geographically, as the intervening section of the North-West Coastal Highway is poorly collected.

Demansia rufescens is geographically closest to D. calodera, with both species known from single specimens



Fig. 16. Holotype of Demansia rufescens (WAM R52747).

among early collections from "Marilla". *Demansia rufescens* lacks the pale edged, dark nuchal band of *D. calodera* (although there is some trace of an obscure dark nuchal mark in two recently collected *D. rufescens* from Hermite Island), and has generally more ventral scales (176–200, mean 190.4 *vs* 171–189, mean 180.4).

Demansia flagellatio, D. quaesitor and D. rimicola all differ from D. rufescens in possessing a dark nuchal collar. Each species also has unique aspects of coloration of the nuchal, temporal or anterior ventral region that are not present in D. rufescens. All three also have much greater numbers of subcaudal scales than D. rufescens, while D. flagellatio also has more ventral scales.

While *D. rufescens* and *D. olivacea* both lack dark nuchal bands, *D. rufescens* does not possess the median series of dark spots on the anterior ventral scales of the latter species, and has fewer subcaudal scales.

Specimens examined. All localities are in Western Australia: AM R100047, Yampire Gorge, Hamersley Range; BMNH 1955.1.4.62, WAM R102362, R102583, Hermite I., Monte Bello Is.; WAM R536, Marble Bar; R5322, Marilla; R14279, Dolphin I.; R15058, Shaw River; R16504, Pt Hedland (= R15064 from Roebourne, cited by Storr, 1978 fide L. Smith, pers. comm.); R26154, Python Pool; R28070, R48956, R51634, Barrow I.; R28929, Mt Newman; R42992, R73679, Tom Price; R45088, "Mt Stuart" Stn; R52747 (holotype), Marandoo minesite; R55965, Marandoo; R66333, West Angelas; R73544, Dampier; R73860, 30 km S Roebourne; R80808, R102202, Karratha; R81294, 4 km SW Newman; R81835, 50 km N Nanutarra; R95285, 6 km S Roebourne; R95337, Burrup Peninsula; R102804, 20°40'45"S 116°45'15"E, Burrup Peninsula; R108820, Mt Princep; R127732, 5 km S Mt Tom Price; 132216, Old Onslow; R132543, "De Grey River" Stn; R132672, Burrup Peninsula.

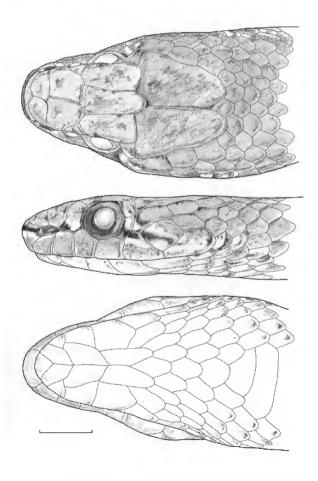


Fig. 17. Head shields and colour pattern of the head and neck of holotype of *Demansia rufescens* in dorsal, left lateral and ventral views. Scale bar = 3 mm.



Fig. 18. Holotype of Demansia shinei (NTM R6489).

Demansia shinei n.sp. Shea

Figs. 18–19

Type material. HOLOTYPE NTM R6489, Frewena, NT, in 19°25'S 135°24'E, collected 18.iii.1979 by P. Horner, J. Griffiths & K. O'Brien, from under rubbish near the roadhouse. PARATYPES. All 23 other specimens listed as specimens examined.

Diagnosis. A medium-sized *Demansia* (SVL up to 622 mm) with brown nuchal collar edged anteriorly and posteriorly with lemon-yellow, a dark teardrop across the fourth and fifth supralabials, ending about junction of last two supralabials, and edged posteriorly with a broad lemon-yellow line that extends onto the primary temporal, throat immaculate or nearly so, and body venter uniformly pale.

Description. Head dorsum and nape mid-brown; narrow dark brown transrostral streak, weakly and narrowly edged above and below with lemon-yellow; dark brown teardrop marking ventrocaudal to eye, beginning broadly at orbit across fourth supralabial and ventral third of lower postocular, arcing narrowly across lower half of fifth supralabial, and ending about junction of fifth and sixth supralabial, temporolabial and lip; a prominent lemon-yellow preocular bar, separating dark transrostral streak from orbit, extending posteroventrally to edge the dark teardrop anteriorly; prominent broad lemon-yellow postocular bar over both postoculars, ventral corner of parietal, anterior third of primary temporal, upper third of fifth supralabial, lower half of temporolabial and extensively onto sixth supralabial, posteriorly edging the dark teardrop. This pale marking continuous with a yellow nuchal band, across caudal edge of parietals and first one or two rows

of nuchal scales, lateroventrally broadening to cover the first three rows of scales posterior to supralabials, and interrupting the brown head colour to leave a brown nuchal band covering 4–5 dorsal scale rows, with irregular margins. Posterior to this, a narrow, one scale wide undulating yellow band, becoming a little wider lateroventrally.

Body dorsum pale grey-brown, with a yellow-brown flush on tail. Ventrolaterally, grey-brown pigment tends to be concentrated increasingly to scale centres, producing a weak striped effect.

Venter pale yellow, gular scales immaculate or with obscure pale grey lateral edges to genials. Margin between greyish flanks and yellow belly not sharp, lying on lateral edges of ventral and subcaudal scales.

Ventrals 177–207, mean = 193.6, s.d. = 8.69, n = 23; subcaudals 69–99, mean = 85.7, s.d. = 7.97, n = 22. SVL 173–622 mm, mean = 427.2 mm, s.d. = 128.0 mm, n = 23; TL 28.0–37.1% of SVL (mean = 33.1%, s.d. = 3.0, n = 22).

Sexual dimorphism. There are no significant differences between males and females in number of ventral scales (males: 177–207, mean = 193.6, s.d. = 8.69, n = 13; females: 177–204, mean = 194.3, s.d. = 8.23, n = 8; t_{19} = -0.166), subcaudal scales (males: 69–99, mean = 87.0, s.d. = 8.71, n = 12; females: 69–96, mean = 83.5, s.d. = 7.54, n = 8; t₁₈ = 0.927), SVL (males: 285–622 mm, mean = 474.7 mm, s.d. = 95.8, n = 13; females: 173–550 mm, mean = 384.3 mm, s.d. = 141.9, n = 8; U = 72) or relative tail length (males: 29.3-37.0% of SVL, mean = 34.1%, n = 12; females: 28.0-36.5%, mean = 31.7%, n = 8; U = 72). The lack of significance could be partly due to the small sample sizes, as the ratio of mean male/mean female relative tail length (1.076) is within the range of variation for the five species for which the difference between means is significant (1.061–1.131), all of which have larger sample sizes. However, it is possible

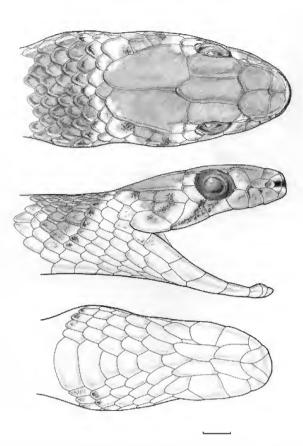


Fig. 19. Head shields and colour pattern of the head and neck of holotype of *Demansia shinei* in dorsal, right lateral and ventral views. Scale bar = 2 mm.

that the lack of significance might be real in some cases, as the ratio of mean male/mean female subcaudal scales (1.042) is lower than for the other seven species for which data are presented in this paper (1.067–1.168), all of which are significantly different.

Etymology. Named in honour of Prof. Rick Shine of the University of Sydney, in appreciation of his extensive studies on Australian elapid ecology, including *Demansia* (Shine, 1980).

Nomenclatural history and description of holotype. *Demansia shinei* was first reported in the literature by Hoser (1989), who provided a photograph of a specimen from Three Ways under the name *D. torquata*. The male holotype (Figs. 18–19) has 189 ventrals, 86 subcaudals, SVL 474 mm and tail length 166 mm.

Distribution. Northern central Australia, from Hall's Creek in the west, to Borroloola in the east, and south to 4 km N Ayer's Rock (Fig. 13). Two additional specimens (WAM R102712, Site Savoury 2, in 23°53'S 120°36'E, Little Sandy Desert, WA; R127178, Nifty Mine, WA) from further south-west, are tentatively assigned to this species, although excluded from the paratype series.

Geographic variation. The two southwesternmost specimens (WAM R102712, R127178) are similar to other specimens in scalation and proportions (ventrals 187, 186 respectively; subcaudals ?, 73; SVL 435, 312 mm; tail length ?, 125 mm) and in the position and extent of the dark teardrop marking, but differ in the weaker dark nuchal collar, and in the narrower pale postocular bar, which does not extend to the temporal scales.

Excluding these two specimens, there is no significant relationship in *D. shinei* between latitude and number of ventral scales ($r^2 < 0.001$, n = 22; $F_{1,20} < 0.001$), subcaudal scales ($r^2 = 0.017$, n = 21; $F_{1,19} = 0.337$), SVL ($r^2 = 0.039$, n = 22; $F_{1,20} = 0.805$) or relative tail length ($r^2 = 0.003$, n = 21; $F_{1,19} = 0.050$).

Comparison with other species: The nature of the head markings in D. shinei is unique, particularly the broad lemon-yellow postocular bar. The distribution of the species extensively overlaps that of D. rimicola, with the two species known to co-exist at Frewena and Elliot. Demansia shinei may be readily differentiated from D. rimicola by the absence of both distinct gular markings and paired rows of dark spots on the anterior ventrals, the much broader and less constricted pale postocular marking on the face, which reaches the throat, and the much less prominent dark marbling on the head dorsum. From the uncollared species, D. angusticeps, D. olivacea and D. rufescens, it is differentiated by the presence of a distinct pale-edged collar, and from D. olivacea it is further differentiated by the absence of a median row of dark spots along the anterior ventral scales. It is differentiated from D. calodera by the width of the pale postocular bar and pale anterior nuchal band, larger size and greater number of ventral scales.

Specimens examined. AM R80532, 4 km S Renner Springs on Stuart Hwy, NT; R165987, "Birrindudu", NT; MV D51847, NTM R8501, R32384–86, Three Ways, NT; NTM R3806, no data; R5819–20, R6488, R7003, R8415, R32392, Frewena, NT; R8543, "Alroy Downs", NT; R9528, 40 km E Frewena, NT; R12470, 4 km N Ayer's Rock, NT; R16598, Yuendumu rd, NT; R32388, Borroloola, NT; R32393, SAM R14029, Elliot, NT; QM J26983, MIM mine, McArthur River, NT; WAM R28072, Hall's Creek, WA.

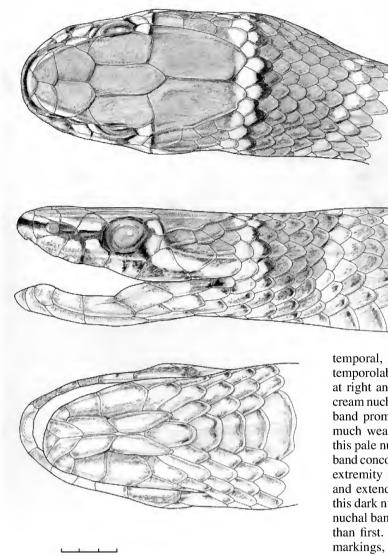


Fig. 20. Head shields and colour pattern of the head and neck of *Demansia torquata* (AM R114086) in dorsal, left lateral and ventral views. Scale bar = 3 mm.

Demansia torquata (Günther, 1862)

Figs. 20-21

Diemenia torquata Günther, 1862: 130. Holotype: BMNH 1946.1.17.41, from Percy I., Qld, collected by F.M. Rayner.

Diagnosis. A medium-sized *Demansia* (maximum SVL 636 mm) with a pale-edged dark nuchal collar (obscure in adults), prominent transrostral streak extending to orbit, prominent pale preocular and postocular bars, the latter not (or barely) reaching throat due to contact or near contact between dark teardrop marking and nuchal collar (the contact of the dark markings may be less intensely dark than the main pattern elements; Fig. 20), and a dark blue-grey belly, at least posteriorly.

Description. Head dorsum and nape dark brown, distinctly darker than body (juveniles) to mid olive-brown and concolorous with body (adults); dark brown transrostral streak, strongly (juveniles) to weakly (adults) creamedged above and below, extending posteriorly to orbit and variably along sutures between first three supralabials; dark brown teardrop posteroventral to eve, beginning broadly over ventral half of lower postocular and posterodorsal corner of fourth supralabial, narrowly arcing over centre of fifth supralabial, ventral corner of temporolabial, ventral margin of sixth supralabial, then over last two infralabials (6/7) and scale rows 2 and 3 on neck; cream preocular bar, interrupted by orbital extension of dark transrostral bar, continuing posteroventrally to edge dark teardrop anteriorly; strong cream postocular bar of even width across anterior half of upper postocular, dorsal half of lower postocular, ventral corner of primary

temporal, dorsal third of fifth supralabial, ventral half of temporolabial and centre of sixth supralabial, before joining, at right angles, a narrow (half to one scale wide) straight cream nuchal band over first scale series on nape; pale nuchal band prominent and sharply defined in juveniles, usually much weaker or even absent in large adults; posterior to this pale nuchal band, a broad (4–5 scale wide) dark nuchal band concolorous with head or a little darker, its ventrolateral extremity continuous or nearly so with the dark teardrop and extending to at least second scale row, if not to first; this dark nuchal band posteriorly bordered by a second pale nuchal band equal in width or a little wider, but less straight than first. In those large adults which have reduced nape markings, the lateroventral extremities of this band persist the longest.

Body mid brown to dark grey-brown, more brown to yellow-brown on tail.

Throat yellow, immaculate or with gray clouding and streaking, particularly along the suture between genials and infralabials; body venter varying from yellow to dark gray, the latter consistently posteriorly, but often as far anteriorly as the anterior ventrals. The change from yellow to grey occurs by progressive posterior development of gray bases to ventral scales. On some individuals, independent of the degree of overall ventral darkening, a median line of darker grey streaks along body venter. Tail venter progressively yellower distally.

In life, one specimen (QM J66807) had the pale periocular markings tinted pink, the ventrals and first three scale rows tinged red, and dorsal scales olive-green with fine pink edging (P. Couper, pers. comm.). Bright pink-red ventrals and first two to three scale rows were also present on a live individual photographed from Airlie Beach (R. Sadlier, pers. comm.).

Ventrals 185–214 (mean = 200.1, s.d. = 5.80, n = 85); subcaudals 76–106 (mean = 87.9, s.d. = 6.60, n = 77). SVL 171–636 mm (mean = 397.4 mm, s.d. = 144.5 mm, n = 83); TL 26.1–38.7% of SVL (mean = 31.8%, s.d. = 2.6, n = 75).

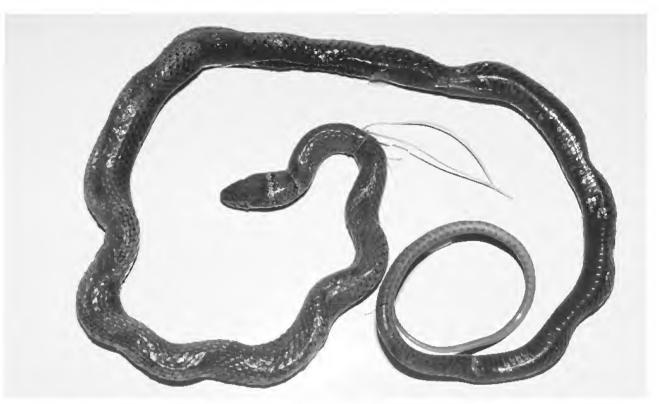


Fig. 21. Holotype of Demansia torquata (BMNH 1946.1.17.41).

Sexual dimorphism. Males have significantly greater numbers of ventral (192–214, mean = 201.7, s.d. = 5.71, n = 46) and subcaudal scales (82–106, mean = 91.5, s.d. = 6.04, n = 41) than females (ventrals: 185–207, mean = 197.5, s.d. = 5.45, n = 32; t_{76} = 3.229**; subcaudals: 76–92, mean = 83.3, s.d. = 3.95, n = 29; t_{68} = 6.377***), and have significantly longer tails (TL: males: 27.4–38.7% of SVL, mean = 32.8%, n = 40; females: 26.9–35.0%, mean = 30.6%, n = 29; U = 868***). The disparity in size between males and females is barely significant (SVL: males: 171–636 mm, mean = 434.2 mm, n = 45; females: 186–593 mm, mean = 369.0 mm, n = 32; U = 933*).

Nomenclatural history and Redescription of holotype. Diemenia torquata was described from a single specimen (BMNH 1946.1.17.41) from the Percy Islands, collected by Frederick Rayner, surgeon on board the Herald on her 1852–1861 voyage to Australia and the southwest Pacific. The specimen was probably collected in July 1859, when the Herald spent three weeks in the Percy Islands (David, 1995). The paper describing the species was published in two parts, the first, including the introduction, in January 1862, the second, with the description of D. torquata, published February 1862. In the introduction, the species is listed as one of a number of new species procured by the British Museum between 1858 and 1861, but with the locality Norfolk I. against the name, although the description gives the type locality as Percy Islands. Similarly, a loose paper label in the jar with the holotype gives the locality as Norfolk I. (GMS, pers. obs.). This locality is in error, as no elapid is known from Norfolk I. (Cogger et al., 1983). The Herald expedition stopped at both islands, and the two conflicting localities probably represent poor labelling of the collections made. Rayner was not appointed as naturalist for the voyage, but took over that task following the dismissal of the appointed naturalist John MacGillivray for misconduct in 1855, prior to the expedition visiting both island groups (David, 1995).

The holotype (Fig. 21) is a typical adult specimen of the species, with 199 ventrals, 83 subcaudals, SVL 443 mm, TL 143 mm. Günther (1862) gives 206 ventrals and 84 subcaudals, probably reflecting different reference points.

Etymology. Presumably from the Latin *torquatus* (collared), and alluding to the nape markings.

Distribution. Coast and ranges of eastern Queensland, from "Batavia Downs" Station in the north to Mt Larcom in the south, and including Fantome, Palm and Magnetic Islands near Townsville, Hayman, Hook, Dent and Long Islands in the Whitsunday Group, Penrith I. in the Cumberland Group, and the Percy Isles (Fig. 10). A single specimen from Savage Creek, Qld is presumed to be from the creek of that name at 20°11'S 143°20'E in the Queensland Museum database. This locality is distant from other localities, and must be regarded as suspect until additional specimens from the same region become available. Numerous literature records from western Queensland, northern NSW and the Northern Territory (Worrell, 1963; Cogger, 1975; Longmore, 1986; Hoser, 1989; Gow, 1989; Swan et al., 2004; Wilson, 2005) are based on other species, particularly D. rimicola, D. quaesitor, D. shinei and D. flagellatio. The record of this species from "Waroora", WA, reported by Cogger (1975) is based on D. calodera.

Geographic variation. Because of the sexual dimorphism in scalation, size and relative tail length, sexes were separated for analyses of patterns of geographic variation.

Males show significant latitudinal effects on number of ventral scales ($r^2 = 0.403$, n = 42; $F_{1,40} = 26.979^{***}$; ventrals = 228.686 - 1.464*latitude), subcaudal scales ($r^2 = 0.403$, n =

37; $F_{1,40} = 23.606^{***}$; subcaudals = 119.115 - 1.503*latitude), SVL (r² = 0.121, n = 41; $F_{1,39} = 5.387^*$; SVL = 829.180 -20.968*latitude) and relative tail length (r² = 0.449, n = 36; $F_{1,34} = 27.725^{***}$; tail length/SVL = 0.455 - 0.007*latitude). In all cases, southern individuals had generally lower values than northern individuals. Examination of plots of each variable against latitude suggests that for number of ventrals, subcaudals and relative tail length, the relationship is stepped, with a sharp change at approximately 19–20°S (near Townsville). This is particularly marked in the case of number of ventrals, where counts of more than 200 are only found north of 20°S, while counts of less than 200 are only found south of 19°S.

This pattern is not apparent for females for most variables. There is no significant latitudinal effect on number of ventrals ($r^2 = 0.000$, n = 29; $F_{1,27} = 0.001$), SVL ($r^2 = 0.044$, n = 29; $F_{1,27} = 1.256$) or relative tail length ($r^2 = 0.042$, n = 27; $F_{1,25} = 1.095$). However, there is a significant relationship between number of subcaudal scales and latitude ($r^2 = 0.227$, n = 27; $F_{1,25} = 7.323^*$; subcaudals = 97.941 - 0.762*latitude), with counts below 83 only occurring in the south of the range, from 18°40'S.

Comparison with other species. *Demansia torquata* is geographically disjunct from all other *Demansia* with collared nape markings. It is geographically closest to *D. rimicola*, but differs from that species in having the pale upper edge of the dark "teardrop" marking on the side of the face continuing as a pale line of even width to join with the pale anterior margin to the nape band, and in lacking the paired series of dark spots on the anterior ventrals. Further, *D. torquata* has a generally greyish hue to the ventral scales in preserved material that is absent in *D. rimicola* and all other collared *Demansia* species (*D. calodera*, *D. flagellatio*, *D. quaesitor*, *D. shinei*), and has higher numbers of ventral scales than all but *D. flagellatio*. The pale nape markings in *D. flagellatio* are much broader than in *D. torquata*, those of *D. calodera* are broader laterally (vs

of even width across the nape), and the dark nape band of *D*. *quaesitor* lacks pale edges.

In addition to the presence of a pale-edged dark collar, *D. torquata* differs from the three uncollared species, *D. angusticeps*, *D. olivacea* and *D. rufescens*, in its greyish venter and greater number of ventral scales. It further lacks the median row of dark spots along the anterior ventral scales that is present in *D. olivacea*, and has well-developed pale edges to the dark "teardrop" that are absent or reduced in *D. olivacea*.

Specimens examined. All localities are in Queensland: AM R7306, Mt Mulligan; R9327, Mt Morgan; R11325, R11728-29, Hayman I.; R12472-73, BMNH 81.10.12.87, Qld; AM R16137, Cairns district; R16764, R16771, Magnetic I.; R47969, Box Ck, Mt Dryandra; R48105-06, Mt Dryandra; R56748-49, Black Mtn; R62709, D8079, Hartley's Creek; AM R62741, Penrith I.; R66268, Bare Hill, Atherton Tableland; R81166, 3.2 km SE Chillagoe P.O.; R81167, ESE side Mt Simon, c.24.8 km S Cooktown P.O.; R92528, SW Mt Garnett, between turnoffs to Mt Surprise; R111903, Haunted Tower, 12.3 km W Chillagoe; R114086, E side Hervey Range; R119465, 6 km along Brandy Creek rd, 10 km W Airlie Beach; R128189, "Batavia Downs", Wenlock River; R128827, R128842, Mt Carbine; R128844, Mandalee, Innot Hot Springs; ANWC R2713, McKenzie River, Edungalba; BMNH 79.8.11.19, Rockhampton: MV R12819, Endeavour River; R12859, Trinity Bay; QM J954, ?Qld; J4191, foot of Berserker Mtns, N of Rockhampton; J4261-62, N Old; J4690, Moore Ck, Rockhampton; J5135, Mossman; J5289-91, J7378, Palm Is.; J5949-50, J37858, Percy Is.; J7930, Archer Pt, 16 km S Cooktown; J11484, Animal Health Stn, Oonoonba, Townsville; J13441, nr Post Office Hotel, Chillagoe; J16650, J19329, Mt Molloy; J24473, Savage Ck; J26296, 13 km S Coen; J28800, Cannonvale Beach via Proserpine; J30782, Walkamin via Mareeba; J31708, Airport Lake base, Cape Flattery mine site; J32283, Shute Harbour; J32383, McIvor River, N of mouth, half way along Mission Rd; J32744, adjoining site 13, Brandy Ck; J33508, Long I., Whitsunday Group; J33940, "Homevale" camp site; J35031-34, Dent I.; J39821, 1.5 km S Coen; J40928–29, J58976, S Percy I.; J45358, summit Mt Mulligan, 3 km SW Mt Mulligan township; J50743, St Pauls Scrub, "Mt Cooper" Stn, Longspring; J51590, 4.3 km along Mt Stuart Rd, nr Townsville; J52890, 6 km N Mareeba; J54130, Emerald Ck nr Mareeba; J55237, Fantome I., Palm Is.; J55238, Castle Hill, Townsville; J55239, Mt Elliot NP, S of Townsville; J55240, Stanton Hill, North Ward, Townsville; J59907, base of Mt Larcom; J62460, Cape Melville; J64870, J65144, Cape Upstart; J66807, Cannonvale, Airlie Beach; USNM 166106, Hook I.

A dichotomous key to the species in the genus Demansia

1	Ventrals 160 or fewer – Ventrals 161 or more	
2	 Anterior ventrals each with a dark median spot or streak, aligning to form a broken narrow median dark line Anterior ventrals lacking a dark median spot or streak (anterior ventrals either unmarked, with a dark posterior edge, or with a pair of dark spots) 	D. olivacea
3	Anterior ventrals each with a pair of dark spots, aligning to form a pair of posteriorly diverging broken dark lines – Anterior ventrals either unmarked, or with a dark posterior edge	
4	One or more dark collars on the nape, becoming less distinct with age – No trace of dark collars on nape in either juveniles or adults	
5	Dark collar(s) on nape distinctly pale-edged (in adults with only weakly distinct collars, pale edging persists longest on lateral sides of nape)	6
	- Dark collar(s) on nape lacking pale margins anteriorly and posteriorly	

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6	Pale anterior edge to broadest dark nape collar several scales wide (on caudal edge of parietals and first two or three series of dorsal scales); pale posterior edge to broadest dark nape collar in turn followed posteriorly by a narrow bold dark collar	D. flagellatio
	posteriorly by dorsal body ground colour	
7	Pale anterior and posterior edges of dark nape collar are of even width dorsally and laterally; ventrolateral extremity of dark nape collar appears to be continuous with, or nearly continuous with, dark suborbital teardrop marking; body venter tends to be dark (in preservative)	D. torquata
	 Pale anterior and posterior edges to dark nape collar broaden laterally; ventrolateral extremity of dark nape collar widely separated from dark suborbital teardrop marking due to pale anterior edge of dark collar blending with pale ventral coloration; body venter pale 	
8	Pale postocular marking broad (extending onto primary temporal); ventrals 177–207 (mean = 193.6); subcaudals 69–99 (mean = 85.7)	
	- Pale postocular marking narrow (confined, in its dorsal section, to postocular scales); ventrals 171–189 (mean = 180.4); subcaudals 65–89 (mean = 76.2)	
9	Dorsal body scales evenly dark brown to black (sometimes paler in juveniles); ventral scales mostly dark grey; dark transrostral streak generally lacking (when weakly present, lacking pale margins).	
	- Dorsal body scales paler (usually greenish, reddish, or grey-green), sometimes with dark apices or bases; ventral scales pale (yellow to cream, with or without a grey-green tinge medially); dark transrostral streak present (though sometimes only weakly defined) and pale-edged	11
10	Ventral scales 197 or fewer; adult snout-vent length up to 1080 mm (males) or 926 mm (females)	D. vestigiata
	- Ventral scales 198 or more; adult snout-vent length up to 1545 mm (males) or 1245 mm (females)	D. papuensis
11	Dark teardrop marking below eye short, ending on fifth supra- labial, rarely extending onto lower extremity of temporolabial	
	- Dark teardrop marking below eye long, extending across fifth supralabial and lower extremity of temporolabial, well onto sixth supralabial	
12	Dorsal scales evenly grey-green, or with a broad russet vertebral stripe anteriorly	D. psammophis
	russet vertebral stripe anteriorly	D. reticulata
13	Distribution Western Australia - Distribution Queensland	
14	Body dorsum greenish; subcaudal scales more numerous (males 80–98; females 74–91)	D. angusticeps
	- Body dorsum reddish; subcaudal scales less numerous (males 65–85; females 65–77)	

Discussion

With recognition of ten species among the material previously ascribed to *D. olivacea* and *D. torquata*, it is germane to consider the identity of material covered in previous taxonomic work. The identity of published photographs is covered in the accounts of the various species.

The first published illustration of D. torquata was by Günther (1862), who illustrated the head of the holotype. However, the illustration was published in the first part of the paper, one month prior to to the textual description of the species in the second section, and as part of a plate including eleven other species, it was readily overlooked. This illustration, although largely accurate in the position and shape of markings, emphasized only the margins of the nape bands, creating the false impression that the dark nape band was pale-centred. Kinghorn (1932) identified as D. torquata both true D. torquata specimens from Percy Island and Mt Morgan, and material from southwestern Queensland which we identify as D. rimicola. It is curious that Kinghorn reported that "except in size, the southwestern specimen does not differ from the typical form". The first published illustration of D. torquata readily available to local researchers, by Kinghorn (1929), appears to be a composite of both of these species. Kinghorn (1929) also used a painting of the New Guinea elapid Aspidomorphus muelleri as his illustration of D. ornaticeps (Cogger, 1967). Given the confusion created by these first published illustrations, and the wide geographic coverage but few specimens available at the time, it is not surprising that Loveridge (1934) (who did not have access to specimens of D. olivacea, D. torquata or the new taxa described in this paper) and Kinghorn (1942) felt that the species boundaries were unable to be defined. Mitchell (1955) followed this lead, referring two specimens of D. olivacea to D. psammophis psammophis. It is only by the examination of large series of specimens that we have been able to identify the constancy in colour pattern elements across wide geographic regions, together with the subtle differences in ventral and subcaudal counts that assist in identifying species. Storr (1978) was also able to use larger series than previously available to identify distinct species within Demansia. However, in largely restricting his study of material to Western Australia, he was unable to make use of broader comparisons across northern Australia when it came to distinguishing species in the Kimberley. Having only 22 specimens from this region, and with most of these from the west Kimberley, he considered that all were assignable to a single taxon, D. olivacea olivacea. However, his description of this taxon abounds in variation in coloration and qualifiers ("usually", "sometimes", "with or without"), and it is now apparent with larger samples and broader comparisons that Storr's single Kimberley taxon is a composite of at least six species. His specimen from "Mt House" (WAM R45688) has been previously identified as a juvenile D. papuensis (Shea, 1998), the Halls Creek specimen (WAM R28072) is D. shinei, his material from Lake Argyle (WAM R42809, R55900–01) represents both D. quaesitor and D. rimicola, and the residue includes both D. olivacea proper and D. angusticeps.

It is also now apparent that the ecological studies of Shine (1980), using Australian Museum and Queensland Museum material, are based on composite samples representing more than one species, at least for his data on *D. olivacea*, *D.*

Shea & Scanlon: tropical whipsnakes

Although this revision resolves most of the residual uncertainty in the alpha-taxonomy of the genus (although there has still not been a thorough revision of variation in the D. psammophis/reticulata complex throughout its range and resolution of the status of the taxa within it; see, for varying treatments, Storr, 1978; Storr et al., 1986; Hutchinson, 1990; Hutchinson & Tyler, 1996; Robinson et al., 2000), phylogenetic relationships among the species of *Demansia* remain unknown. There is no suggestion from the complex mosaic of states among the external characters we have used to distinguish species that either the collared or uncollared taxa form clades, nor are there any obvious covarying patterns in morphology among species. Among scale counts that vary between species, number of ventrals is highest in D. papuensis and D. flagellatio, with D. torquata nearly as high, while D. simplex and D. olivacea have the lowest counts. However, sexual dimorphism in number of ventral scales has thus far been demonstrated only in D. papuensis, D. torquata and D. olivacea, representing the extremes of ventral scale number for taxa for which comparisons are yet possible (no data are available to test for sexual dimorphism in D. simplex or D. flagellatio). In all three cases, males have greater mean numbers of ventral scales than females. In number of subcaudal scales, significant sexual dimorphism is standard for all taxa represented by adequate samples, with the mean for males being consistently higher than the mean for females (ratio of male/female means ranges from 1.042-1.168 for the nine species for which data are provided herein, together with D. papuensis and D. vestigiata; data from Shea, 1998). In the middle of this range are the two species with the lowest numbers of subcaudal scales (D. calodera and D. rufescens, ratio of means 1.100 and 1.080) as well as two species with high numbers of subcaudal scales (D. papuensis and D. torquata: ratio of means 1.095 and 1.098).

With the addition of the new species described in this paper, *Demansia* becomes the most species-rich genus of Australian elapids, yet one with a highly conserved general morphology. Despite this morphological conservatism, the species in the genus are commonly sympatric. In particular, the east Kimberley region has the greatest diversity of *Demansia* species, with eight taxa occurring there (*D. angusticeps, D. quaesitor, D. olivacea, D. papuensis, D. rimicola, D. shinei, D. simplex* and *D. vestigiata*; Storr, 1978, Shea, 1998). This coexistence of morphologically similar elapid snakes is unparalleled among other Australian elapids, and if a well-supported phylogeny becomes available when internal characters and genetic evidence are included, then the genus has the potential to be a useful model system for evolutionary and ecological studies.

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[* Kinghorn misnumbered this paper. It should have been No. 5 in his series titled "Herpetological Notes"]

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